Community ecology and conservation of tropical rainforest birds in the southern Western Ghats, India

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DEDICATION

I dedicate this thesis

To

Sitalakshmi Rajagopalan & T. R. Rajagopalan,

who brought me to the beginning of this journey,

R. K. G. Menon,

who pointed the way

&

Divya Mudappa,

who made the journey wonderful and worthwhile.

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Is it really worth while to spend our time, the time which escapes us so swiftly, this stuff of life…in gleaning facts of indifferent moment and highly contestable utility? Is it not childish to inquire so minutely into [a creature's] actions? Too many interests of a graver kind hold us in their grasp to leave leisure for these amusements. That is how the harsh experience of age impels us to speak; that is how I should conclude…if I did not perceive, amid the chaos of my observations, a few gleams of light toughing the loftiest problems… [These] will be the despair of every cultivated mind, even though the insanity of our efforts to solve them urges us to cast them into the limbo of the unknowable.

–J. Henri Fabre

CHAPTER 1

Introduction

Life is simple and complex at once. We sense it with a mingled perception, garnering minutiae of detail describing the biology of life while at the same time striving to encompass within our understanding phenomena whose scale is limited, perhaps, only by the width of our imagination. Thus, the flood of sunlight from outer space energising the great engines of life on Earth is of as much interest and import as the dance of sun-flecks that spell life and death for plants on the forest floor. And similarly, the study of the structure of a protein molecule in our blood is as much a part of our developing understanding as is the study of how we, as a species, are altering the face of the Earth and its functioning.

Interactions between organisms and their physical and biological environment, which is the stuff of ecology, take myriad forms. Some may be truly random, fluctuating with the vagaries of chance. Many may appear random, but in reality be pre-ordained by a multitude of intermeshed forces difficult to disentangle and comprehend. And fewer are those that are clearly predictable, guided by factors that can be observed, measured, and tangibly understood. The science and art of observing, measuring, understanding, and predicting complex natural phenomena presents the greatest challenge to ecologists.

1.1 Why study communities?

Community ecology is a front-runner among the challenging fields of research in biology. This is primarily for two reasons. The first is complexity. Many ecological processes interact to determine the structure of communities, presenting a provocative field of enquiry aimed at probing and establishing the relative influence of different factors. The second is utility. No field biologist would today deny that the world faces a major extinction crisis, whose pace and magnitude, dictated by human action, is unparalleled in the Earth's evolutionary history. In the light of global onslaughts on natural habitats and the surge of interest in conserving the diversity of life on our planet, biological

communities represent useful foci for conservation research and action. Individual species differ in their responses to human disturbances and therefore communities, which represent sets of species, often enable a better and more holistic assessment of the effects of such disturbances.

Fundamental to the study of communities is the description of the species they include, the abundances of these species, ranging from the common to the rare, and the variations in these attributes over space and time—what may be called the *pattern* of community structure. Historically, much of the theoretical work, empirical analyses, and debates in community ecology have focussed on determining if these patterns are predictable results of any underlying factor or ecological *process*. For instance, are the numbers and kinds of species found in an area (pattern) determined by the competition between species for space and resources (process)?

The central debate in community ecology concerns the true nature, stability, and predictability of community structure. The views of biologists have spanned a spectrum between two opposing extremes. Some, following in the tradition of the botanist Frederick Clements, have argued that the structure of a community always attains an *equilibrium*, with a certain number of species and fixed relative abundances. Others, trodding the intellectual trail of Henry Gleason, argue that such constancy is rare in nature and communities are in a state of *non-equilibrium*. This is typically because of random fluctuations in the numbers, kinds, and abundances of species. For instance, the establishment of a native species of tree in a particular community may be virtually certain under Clement's viewpoint, but would depend on the likelihood of seed deposition, germination, and establishment under fluctuating environmental conditions in Gleason's view. An intermediate possibility is what has been called a *dynamic equilibrium*, best enunciated in Robert A. MacArthur and Edward O. Wilson's theory of island biogeography. Here, the number of species in an island is expected to remain constant at equilibrium, because of a perfect balance between immigration and extinction of species. When the number of new species arriving and the number of existing species going extinct are equal, there is no change in the total number of species in the area, although the species composition is dynamically changing all the time. The three processes can be illustrated with a simple analogy. The equilibrium process can be compared to a valve-controlled cistern that always fills up with water to a fixed level. In contrast, the non-equilibrium process is like a bucket kept out to gather rain water, whose level would fluctuate widely depending on rainfall and evaporation. Following the same analogy, the dynamic equilibrium is akin to a leaky bucket, where the water lost through leakage is exactly compensated by water filling the bucket from a tap.

What biologists have mainly debated is whether communities are at equilibrium with their environment as a result of predictable biological processes. Such predictable processes have also been called *deterministic* factors. For instance, the number of species in an area could depend on the specific structure and availability of habitat, or the occurrence of competition between species. On the other hand, communities may be in non-equilibrium, with a dynamic driven by random or unpredictable forces. The number of species in an area, under this situation, would simply depend on

chance events of colonisation or extinction of species. Such chance forces have also been called *stochastic* factors.

This debate over the relative importance of chance *versus* determinism leads on to many questions which need answers. Do similar communities recur on sites with similar environments? Or does the composition of communities change continuously over space and time due to random factors or the distance between sites? After a disturbance event, such as when a forest is logged for timber, do communities recover with time to attain their pre-disturbance composition and structure? Are there any rules specifying how species assemble to form communities? What determines changes in community structure from one place to another, or from one year to the next—factors such as resource availability and climate that can be measured or the influences of chance colonisation and extinction that can be modelled using probability theory, mathematical equations, or computer simulations? Where multiple factors influence community structure, what is the relative importance of different factors and how do they affect each other? Indeed, community structure is unlikely to be purely a result of either deterministic factors such as habitat structure or competition, or random factors such as chance assembly or extinction of species. Instead, most communities are likely to be structured to a significant extent by both determinism and chance, and the question pertinent to specific communities is to what extent the two opposing forces influence observed community structure.

One major approach used to explore such questions in community ecology is the study of changes in community structure along continuously changing gradients. These gradients may extend over time, as when we examine over many years the changes in tree species in a regenerating forest. On the other hand, the gradients may be spatial, such as the changes in environment from the tropical forests near the equator to the ice-covered tundra at the poles. Within tropical regions, much attention has been placed on the changes in plant and animal communities along altitudinal gradients – from the plains and foothills to the summits of mountains. Biologists have predicted that the number of species should decline as one goes from the lowest to the highest reaches of mountain ranges because resource availability and productivity decline with altitude and falling temperatures. Under other conditions, mid-elevation areas are expected to have the most species. The changes in species composition along altitudinal gradients are less clearly understood. Is the change gradual and continuous, or abrupt at particular altitudes due to a sudden change in environment or the appearance of some competing species? Again, to what extent are the numbers or kinds of species found in one particular site along the gradient a consequence of chance factors as opposed to the specific environment of the site? Could the similarity between two sites in the species they contain be a result of the chance accrual of species or because the sites were similar in habitat attributes and therefore attracted the same species?

In this thesis, I ask and attempt to answer some of these questions in community ecology. I describe how communities change along natural gradients and gradients of disturbance created through habitat alteration by humans. In trying to understand the underlying processes that bring

about these changes, I examine whether these changes are due to chance factors or due to other measurable changes in the habitat and environment. In this study, I focus on communities of birds.

1.2 Why birds?

My most direct and straightforward reason for studying birds is that this is simply the group that I am most familiar with, that I most enjoy watching and studying, and whose conservation is of particular concern. Fortuitously though, birds are not a bad choice for studies in community ecology for a variety of reasons.

Until recently, geologically speaking, the Earth had over 10,000 species of birds. With the history of extinctions over the last two millenia, this is down to about 9,600 extant species worldwide. Among all known terrestrial vertebrate groups, birds are the richest in species. This is reflected not only at the global level but also locally—particularly in forest habitats around the world where the number of bird species exceeds the number of species of mammals, reptiles, or amphibians, by at least a factor of two, if not more. This diversity itself is intrinsically of interest to biologists and it is not surprising, then, that a large body of work in ecology has targeted the study of bird communities. How do so many species of birds coexist in an area? How do they partition use of space or resources? How do they affect each other positively, through mutually-beneficial relationships such as flocking, or negatively through competition for territory and food? Why do some areas have far more species than others? Above all, in the face of human-induced changes in their habitats, how can we maintain these rich and interactive communities and keep them from sliding into evolutionary oblivion through extinction? These are some of the questions central to this field of research.

Most birds have distinct plumages and voices, and are active during the day. Thus, with a modest investment in effort, birds are often easily identified and counted in the field, even in densely vegetated tropical rainforest. The field study of birds is thus more workable than, say, an exploration into communities of oribatid mites in rainforest soil or minuscule epiphylls on leaves in the rainforest canopy. Nevertheless, time and effort need to be invested in standardising the methods, field techniques, and developing appropriate analytical procedures. A fundamental need in many bird community studies is to assess different techniques for censusing birds and identify those suitable for particular objectives, areas, or species. An attempt on these lines is featured in this thesis.

The flight and mobility of birds is another key characteristic. Birds may flee a forest being felled as swiftly as they may colonise one that is regenerating. A list of bird species found in an area may indicate to the naturalist the habitats it is likely to contain as effectively as a photograph of the area may bring to mind the birds likely to be found therein. When habitats are altered by human action, this unwittingly acts as a large-scale field perturbation experiment. The creation of islands of habitat through deforestation or development, the recovery of forest vegetation after slash-and-burn agriculture, the hunting to extinction of a species, the creation of large areas of agricultural crops or

timber plantations, or subtler changes brought about by chronic extraction of natural products from ecosystems—these can all be treated as field experiments. Such experiments, of which there has been no dearth—and no foreseeable decline to contend with—form a bedrock of much of the research in this thesis, as in many other field studies of birds.

Although conditions are not strictly controlled in such field experiments, they nevertheless have much to offer a keen observer. The diversity in bird species is reflected in the diversity of their responses to habitat disturbance. A babbler that forages on insects in the forest floor may be expected to respond differently to a disturbance, such as the logging of trees, as compared to a species of woodpecker that forages for insects on tree trunks and nests in tree holes. The removal of forest understorey for a coffee plantation may be expected to affect a species of understorey flycatcher more than a wide-ranging fruit-eating pigeon that visits the fruiting trees in the canopy. Some of these changes may be obvious and direct, leading to the local extinction of a species or the unexpected appearance of another. Others are more subtle and may occur gradually—a change in the abundances of bird species with some declining to become rarer and others thriving in higher numbers, or a bird species hovering at the edge of extinction because of its slow breeding rates or vulnerability to predators and parasites.

How does the diversity of birds or the composition of communities change when humans alter their habitat? What makes some species vulnerable, and others prolific? Identifying which changes in the habitat contribute most to effect changes in bird communities as well as uncovering which traits of bird species render them more vulnerable to extinction are key areas of bird community research. These questions occupy a significant part of this thesis. Due to their remarkable utility as biological 'thermometers' or indicators, the study of changes in communities of birds has given us great insights in the related field of conservation biology.

1.3 The challenges of bird conservation

Our foremost need to have all manner of birds around us is due to their intrinsic value—aesthetic and ethical. A more practical reason is that birds, through their sheer diversity, numbers, mobility, and functional roles as predators, prey, and dispersers of pollen and plant seed, are necessary for the survival of natural ecosystems and for the services that they provide us. Insect-eating birds, often the most abundant in forest ecosystems, perform incalculable service by controlling populations of insects and other arthropods. Even in some man-made habitats, such as coffee estates, the role of insect-eating birds in pest control has been established in recent years. Birds that relish nectar or fruit pulp also move pollen and seed, often over vast distances, performing valuable services vital for plant survival. Their effectiveness in this and their mutual inter-dependence with plants, well established in the case of birds like hornbills, argues strongly for the conservation of bird populations. Many scientists have also noted the direct economic value of birds in the pet and bushmeat trades as an

incentive for conservation, but this is a double-edged sword that can as easily drive a species extinct as save it for, so to speak, human consumption. The task of conservation is not easy as birds face a variety of threats to their survival—loss and alteration of habitats, hunting, the proliferation of exotic species, parasites, and predators, and intrinsic population failure due to poor survival and reproductive rates.

Habitat loss is perhaps the most critical issue for conservation of birds, as it is for most plant and animal species. For instance, between 1981 and 1990, humans deforested over 150 million hectares of tropical forest in the world (representing 9% of the world's tropical forests). Most (85%) of the forest area lost was tropical moist forest, which contains a great proportion of the world's birds and is one the planet's most threatened ecosystems. The effects of habitat loss are often immediate and directly palpable, as when a forest is felled or a lake reclaimed and replaced by human dwellings or agricultural fields. Other forces too are at work, whose consequences may only manifest gradually. The chronic, unregulated extraction of natural produce such as minor forest products and timber, the invasion and spread of exotic species, predators, parasites, weeds, and animals commensal to man—all these are symptomatic of habitat deterioration and can impinge on bird communities.

On the other hand, habitat 'loss' does not always result in the replacement of a natural habitat by one that is sterile or completely unsuitable for birds. Often, man-made habitats such as plantations and crop-fields replace them. In regions of tropical forest, there are innumerable areas today that were abandoned after being used, for selective logging of timber, for creation of plantations, or for agriculture. These areas, usually labelled secondary forest, contain mixed vegetation or forest in various stages of regeneration, and support populations of many bird species, including ones that inhabited the original forest that once stood there. Such areas will, if anything, only increase in extent and spread in the future. Around the world, conservation biologists today recognise the value that such secondary habitats have for wild species. Conservation cannot be restricted to the few pristine ecosystems that may remain but will perforce have to include such areas. There has thus been renewed interest in determining what exactly secondary habitats contain and what potential they hold for conservation. How do bird communities change from pristine to secondary vegetation? Which species are affected by the habitat alteration and why? What attributes of the secondary habitat are crucial for survival of species or the maintenance of bird community structure typical of undisturbed areas? These are some of the questions being asked elsewhere as well as in this thesis.

Another major force of habitat transformation worldwide is considered by many to be the most serious conservation problem we now face. This is the conversion of remaining habitats from large relatively compact and contiguous tracts to a complex of patches, such as pockets of forest in an otherwise denuded and 'developed' landscape—a process that has been labelled *habitat fragmentation*. One of the fundamental questions that arise is the following: is a large tract of forest, say 100 km², equivalent to the same 100 km² existing as ten separate pieces? In a way, the nature

writer David Quammen has answered this question with another: will a 100 m² richly decorated Persian carpet remain the same if it is cut into many small pieces?

The issue is not trivial. Increasingly, most remaining natural habitats occur as fragments. We have to know what fragments contain and how species can be conserved therein, if all or most of the remaining habitat occurs as fragments. How does fragmentation affect rainforests and their bird communities? The biological effects of habitat fragmentation are many. There are environmental changes in temperature, humidity, and wind speeds, which affect plant establishment, growth, and survival. If remnant patches or *fragments* are small, they may be inadequate to meet the year-round space and food requirements of many bird species. Changes are pronounced, particularly along the edges of fragments, and plant and bird species that thrive in the more open, disturbed environment may begin to proliferate whereas shy and specialised species of the rainforest interior may decline.

Fragments of habitat are in many ways similar to islands. The patterns of change in bird community structure from small to large islands are mimicked in these terrestrial habitat 'islands'. Biologists have used a body of theory called island biogeography, or more generally insular biogeography, to elucidate these patterns and probe the underlying mechanisms. Among the predictions of this theory is the observation that an island that is large or close to a source pool (say, a large forest tract) will have more species than an island that is smaller or farther away from the source. In general, with increase in area one expects an increase in the number of bird species. A number of studies around the world have supported this prediction but there have been exceptions and alternative explanations too.

The number of bird species in a fragment may depend instead on the structure of the habitat or the diversity of habitats it contains. The greater number of bird species on larger fragments may be a consequence of this. On the other hand, one could expect that even if birds were colonising fragments at random, large fragments would receive more individual birds than others and, overall, would end up containing more species through a process labelled 'passive sampling'. Besides change in the number of species, the composition of the bird community may also change with fragmentation. Do all small fragments contain the same few species that can thrive in such small areas or do they contain a mix of species depending largely on chance? As forest patches become smaller and smaller, do species become extinct in a random sequence or in a particular order depending on the ecological needs of the species? Few studies have addressed all these questions simultaneously and comprehensively in order to understand which among these alternative mechanisms contains most substance in explaining real-world phenomena. Such studies are useful as they can assist in developing informed strategies for bird conservation. In the final part of this thesis, I address the effects of fragmentation of tropical rainforest on bird communities, within such a holistic perspective, in a biologically unique region in India.

1.4 The Western Ghats

Along the west coast of India, from the River Tapti at 21° N to the southern tip of the Indian peninsula at 8° N, near Kanyakumari, runs the 1,600-km-long chain of hills called the Western Ghats. From the dawn of the Tertiary era at least, some 65 million years ago, the great scarp of the Western Ghats has been a characteristic feature of the Indian peninsula, then a triangular wedge of land moving towards its great collision with the Asian landmass resulting in the genesis of the Himalaya. Undoubtedly, the environment and the plant and animal species found on the land were different then. Prior to the great Cretaceous–Tertiary extinction, the land contained dinosaurs, forms peculiar to India as well as those similar to the dinosaurs of Madagascar and South America. There were similarities with the present-day too: rainforest trees such as *Bischofia, Canarium, Elaeocarpus,* and *Persea*, typical of the wet evergreen rainforests of today, occurred then as now, as evidenced from fossil pollen records.

The Western Ghats has attained recognition as one of the biologically unique areas for conservation in the world. Biologists have included it among the 25 hotspots of biological diversity in the world because of the large number of plant and animal species it contains, including hundreds that are not found elsewhere in the world. In fact, along with Sri Lanka, the Western Ghats is placed among the eight 'hottest' of the hotspots. The Western Ghats has also been recognised as one among the 200 globally most-valuable ecoregions for the conservation of the diversity of life on Earth. Over 4,000 species of plants and nearly 1,000 species of terrestrial vertebrates (amphibians, reptiles, birds, and mammals) are known from the Western Ghats. The diversity of species can be largely attributed to the pronounced variation in environment as one goes from south to north (8° to 21° N), west to east (windward to rain-shadow), and low to high elevations (foothills to 2,600 m). Although the Western Ghats receives precipitation from two monsoons, the southwest or summer monsoon (June to September) and the northeast or winter monsoon (October to January), the rainfall is distributed unevenly. The northern reaches do not receive rainfall from the northeast monsoon and have a long dry season of 5 – 8 months duration. The southern Western Ghats region, south of the Palghat Gap, has a shorter dry season, receiving precipitation from both monsoons. This region is also biologically and topographically more diverse than the northern Ghats. In the drier tracts are tropical dry thorn and dry deciduous forests, the abode of birds such as the Indian Peafowl, Indian Roller, Grey Francolin, Yellow-billed Babbler, and White-bellied Drongo. With increasing moisture come the tropical moist-deciduous, semi-evergreen, and wet evergreen forests, characterised by birds such as hornbills, trogons, laughingthrushes, and frogmouths. Other habitats such as low and high-elevation grasslands, rivers and streams, add their share of species. For birds, the Western Ghats has been recognised as an internationally important Endemic Bird Area, containing 16 bird species with restricted geographical ranges, including 12 species that are considered globally near-threatened.

Like many other regions of the world that are biologically rich and crucial for conservation, the Western Ghats today faces increasing degradation and loss of habitats, and a number of other

threats to the survival of wild species. This is not surprising as, among the global hotspots, this is the hotspot with the highest human population density. Biologists have estimated that, of the original extent of 182,500 km² of natural or primary vegetation that existed in the Western Ghats and Sri Lanka, only 12,450 km² or 6.8% remains. The pace of loss of forest cover intensified during the pre-Independence period under British rule as forests were exploited for timber and converted to extensive plantations of timber, tea, coffee, cardamom, rubber, and pepper. Forest loss continued after Independence due to the continuation of such changes as well as due to agriculture, development, and the creation of large dams and reservoirs for hydroelectric power and irrigation. Between 1920 and 1990, forest cover declined by 40% with a four-fold increase in the number of fragments and an 83% reduction in the size of forest patches. The area under plantations now is also large and growing. For instance, the area under tea plantation, devoid of forest cover, increased from over 74,000 ha in 1987 to nearly 88,000 in 1998.

Few areas remain in the Western Ghats with large unbroken stretches of natural tropical rainforest vegetation; most areas are highly human-altered landscapes dominated by plantations and developed areas with only fragments of forests remaining. Two study areas, both in the biologically richer southern Western Ghats, representing these contrasting landscapes, were selected for this study. The first was the landscape of the Kalakad-Mundanthurai Tiger Reserve containing about 200 km² of relatively undisturbed and contiguous tropical rainforest—one of the largest such tracts left in the Western Ghats. Besides being intrinsically of great interest, this region forms a benchmark, representing near-pristine conditions, against which other areas can be compared. The second area of study, the Anamalai (literally, "elephant hills"), contains tropical rainforests occurring as fragments in a landscape dominated by commercial plantations of tea, coffee, other cash crops, reservoirs, and developed areas. The Anamalai hills offers an instructive case study of the ecological effects of large-scale landscape alteration brought about by human action.

A number of recent studies referred to in this thesis have brought to the fore the ongoing habitat degradation and its detrimental effects on wild plant and animal species. Such ongoing habitat and landscape transformation is of great concern to conservation biologists. We are yet to fully understand their long-term impacts and have only begun identifying ameliorative conservation measures. This thesis is a contribution to this emerging body of work.

1.5 Organization of the thesis

This thesis is organised in seven chapters. In this first chapter, a general introduction is presented on the subject of the research and related fields. For the sake of wider and easier readability, I have abstained from providing detailed bibliographic references and description of theory and methods. These are included in the remaining chapters that constitute the core of the thesis. Chapter 2 describes the study area and study sites selected for this research giving a biogeographic and historical

background. A comprehensive introduction to the specific topics of research, along with details of methods and analysis, is presented along with each of the succeeding four chapters dealing with the major results of the study. Chapter 3 describes methods and results pertinent to the assessment of field census techniques and discusses their utility and drawbacks for interspecific comparisons of rainforest bird densities and bird population monitoring programmes. In Chapter 4, I describe patterns of variation in bird community structure in relatively undisturbed tropical rainforests along an elevational gradient in the Kalakad-Mundanthurai Tiger Reserve. The next chapter examines, in the same area, changes in bird community structure in abandoned plantations, rainforest-plantation edges, and selectively logged areas. The final phase of the study in the Anamalai hills, described in Chapter 6, explores the effects of rainforest fragmentation and conversion to plantations of tea, coffee, and *Eucalyptus*, on the structure of bird communities. Chapter 7 attempts to synthesise and briefly summarise the broad findings and conclusions, contrast the results from the dramatically different landscapes of Kalakad-Mundanthurai Tiger Reserve and the Anamalai hills, highlight conservation implications, and give pointers for future work.

CHAPTER 2

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CHAPTER 2

Study Area

This study was carried out in the Western Ghats hill ranges, recognised as one of the unique and distinctive biogeographic regions within India (Mani 1974, Rodgers and Panwar 1988). This region has also gained international attention as a globally important ecoregion (Olson and Dinerstein 1998) and, along with Sri Lanka, a biodiversity hotspot (Myers *et al.* 2000). The Western Ghats and Sri Lanka region is also the hotspot with the highest human population densities (Cincotta *et al.* 2000).

The following sections describe key features of the entire Ghats, as well as specific study areas in the Kalakad-Mundanthurai Tiger Reserve and Anamalai hills in Tamil Nadu. Details of specific sites selected within these study areas for bird and vegetation sampling are provided in the respective chapters.

2.1 THE WESTERN GHATS

2.1.1 Physiography

The Western Ghats is a 1,600 km long chain of hills running along the west coast of the Indian Peninsula, from near Kanyakumari at 8° N at the southern end to the river Tapti in the north at 21° N (Mani 1974). The Western Ghats, distributed narrowly between 73° and 77° E, is less than 100 km wide over most of its length, being widest in the region of the Anamalai and Nilgiri ranges. Passing through the states of Gujarat, Maharashtra, Goa, Karnataka, Kerala, and Tamil Nadu, a number of hill ranges link up to form the Western Ghats. Going from north to south, this includes the Dangs, the Krishna Ghats, the hills of Uttara and Dakhsina Kannada, Pushpagiri and Brahmagiri, and tall and imposing ranges of the Nilgiri (a meeting point with the Eastern Ghats), Anamalai, Palni, Cardamom (Elamalai), Varushanad, and Agasthyamalai hills (Figure 2.1).

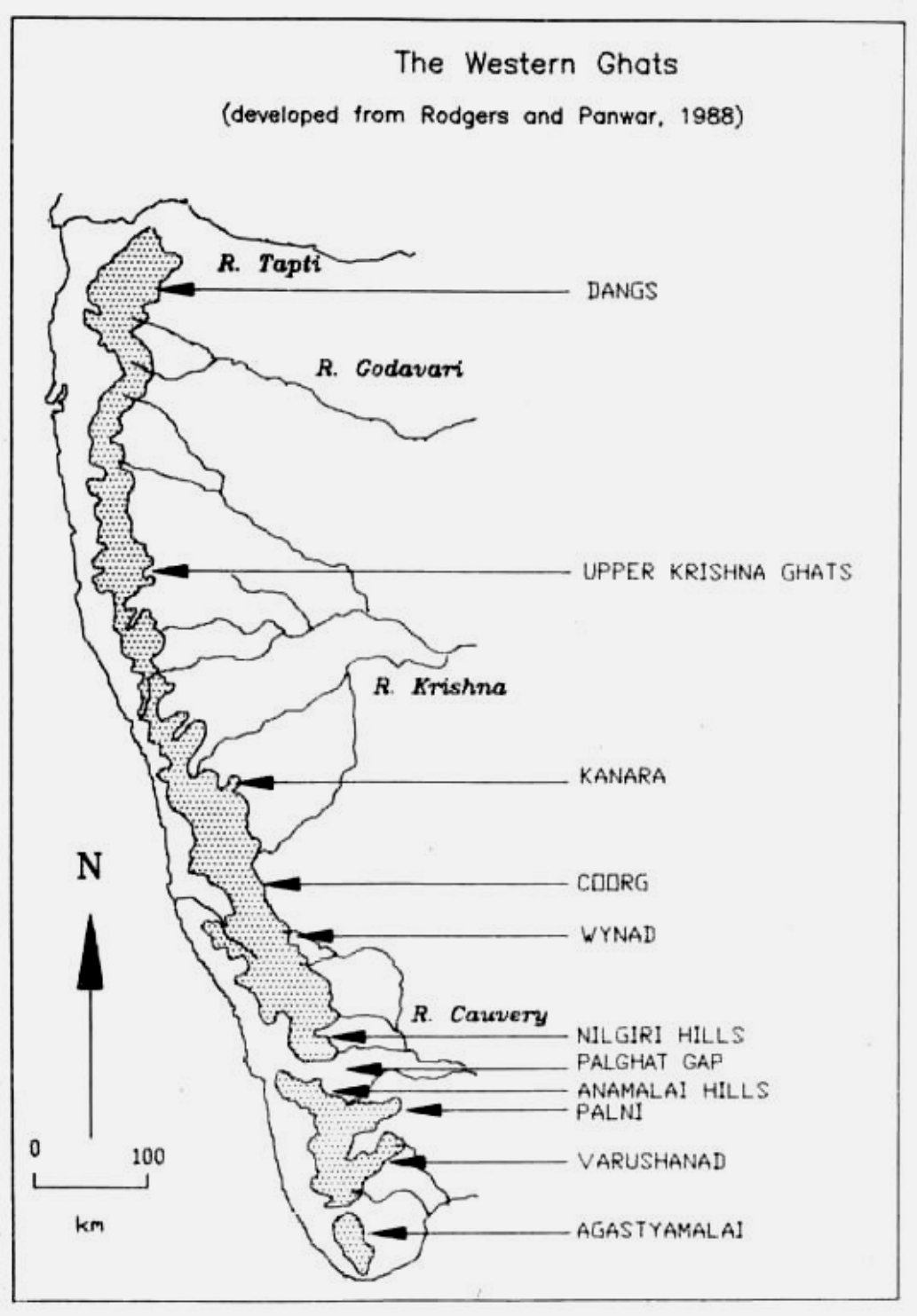

Figure 2.1: Map of the Western Ghats hill ranges along the west coast of India.

The chain of hills is interrupted by the 30 km wide Palghat Gap at around 11° N, and a few other minor breaks along its length (e.g., Shencottah pass at around 9° N, altitude 160 m). Most of the hills over 1,500 m above mean sea level in the Western Ghats are found towards the south, between 8° and 13° N. This includes peaks such as Anaimudi (2,695 m) in the Anamalai hills, Doddabetta (2,637 m) in the Nilgiri hills, Vandaravu (2,554 m) and Kodaikanal (2,328 m) in the Palni hills, and

Agasthyamalai (1,868 m) in the Agasthyamalai range of hills. The region south of the Palghat Gap (see Section 2.1.3), called the southern Western Ghats, is the region of focus in this study.

Several major rivers drain the Western Ghats towards the east, including the Godavari, Krishna, Cauvery, and Tambiraparani. Smaller, more torrential streams and rivers, such as the Kali, Netravati, Sharavathy, Periyar, and Pamba, drain the Ghats from the steeper Western escarpments into the Arabian Sea in the west. These rivers are a major lifeline for millions of people in the plains and foothills being critical for agriculture as well as hydro-electric power generation.

2.1.2 Geology and palaeoecology

From the dawn of the Tertiary era at least, some 65 million years ago (Mya), the great scarp of the Western Ghats has been a characteristic feature of the Indian Peninsula. This was then a triangular wedge of land, a piece of the ancient Gondwana landmass, moving towards its great collision with the Asian landmass that resulted in the orogenesis of the Himalaya (Radhakrishna 1991). It was an island presumably with oceanic, equable climate (Meher-Homji 1989). Around 65 Mya, the northern portions witnessed the enormous volcanic eruptions resulting in the formation of the Deccan Traps—a vast region of over 500,000 km² of basaltic rock, noticeable even today (Sahni 1991). This period of upheaval was followed by a domal uplift that raised the surface of the Peninsula. Faulting occurred along the weaker axial region of the Peninsula, along a line roughly on its central, most elevated region. The portion to the west then slipped and subsided into the sea, leaving the steep escarpment and narrow west coast of the Ghats fringing the Arabian Sea (Radhakrishna 1991, 1993). An alternative view is that the formation of the Western Ghats is related to the revival of tectonic activity in the Deccan as a consequence of the collision with the Asian plate (Pascal 1988).

The rocks and soils of the Western Ghats relate to the region's tectonic history. North of Goa from around 16° N the major geological formation is the Deccan traps overlying Archaean rocks. As Sahni (1991) says, "Even after the continual erosion of millions of years the Deccan traps still cover an area of 200,000 square miles… Their abrupt ending along the west coast, where they are thickest and form the great scarp of the Western Ghats, leaves us no real measure of their original extension into the tract of land that foundered into the Arabian Sea." The Deccan Traps had little influence, however, on the regions south of Goa, which are dominated by the Dharwar system of ancient metamorphic rocks up to about Mangalore (13° N), and pre-Cambrian crystalline rocks further south. In the southern Western Ghats, these are principally charnockites, with Khondalites (gneiss and schists with sillimanite and garnet) dominating south of 9° N (Pascal 1988). The major soils found on the Western Ghats are red soils, laterites, black soils, and humid soils such as the peat bogs of the Nilgiri (Subrahmanyam and Nayar 1974, Nair and Daniel 1986).

The evolving landscape of the Peninsula and the collision with mainland Asia certainly played key roles in the evolution and biogeography of plant and animal species in the Western Ghats.

Prior to the late Creatceous extinctions, the land contained dinosaurs, forms peculiar to India as well as those similar to dinosaurs of Madagascar and South America (Sahni 1991). Although detailed information is lacking, the extent of evergreen forest is likely to have fluctuated from the Eocene to the present-day in consonance with global cycles of warming and cooling (Janis 1993). For instance, during the Miocene, present-day south India was near the equator, with a hot-humid climate and evergreen forests as indicated by palaeomagnetic studies and fossil evidence. These evergreen forests contained taxa similar to the present-day flora: rainforest trees such as *Bischofia, Canarium, Elaeocarpus,* and *Persea* (Meher-Homji 1989). Similarly, from the Miocene age, species such as *Dipterocarpus, Gluta, Hopea,* and *Mesua*, are known from the Pondicherry-Cuddalore area along the south-east coast of the Peninsula. Fossil records of podocarp (conifer-gymnosperm) woods are also available from the Neyveli region from the Miocene; one species of conifer, *Podocarpus wallichianus* (= *Decussocarpus wallichianus* = *Nagaea wallichiana*), occurs in the evergreen forests of Western Ghats even today (Meher-Homji 1989).

More detailed information available for the late Quaternary period from around 40,000 yr before the present (BP) also suggests cycles of expansion and shrinkage of the area under tropical moist forests in the Western Ghats. Available data suggests that tropical moist forests are likely to have been far less widespread during the cold and arid period between 20,000 to 16,000 years BP (Sukumar *et al.* 1995). In contrast, such forests probably expanded and occupied greater areas between 11,000-9,000 yr BP up to the Holocene optimum and again receded during an arid phase between 6,000-3,500 yr BP, with the present-day situation being somewhat intermediate (Sukumar *et al.* 1995, Rajagopalan *et al.* 1997).

2.1.3 Biogeography

The Western Ghats has been long recognised as an important biogeographic region within the Indian sub-continent (Mani 1974). According to Rodgers and Panwar (1988), the Western Ghats biogeographic zone (Zone 5) consists of two biotic provinces: Malabar Coast (5A) and Western Ghat Mountains (5B). The former, stretching all along the western side of the Ghats, consists of the coastal plains and foothills up to the 250 m contour. The moist forests, swamps, and wetlands of this province have been largely denuded or destroyed. The province 5B includes most of the remaining dry and moist forests of the Western Ghats.

The biogeographic distinctiveness of the Western Ghats has been incorporated in two recent global approaches to setting conservation priorities for the world's ecosystems. The *biodiversity hotspot approach* identifies the Western Ghats along with Sri Lanka as among the 25 major tropical wilderness areas or biodiversity hotspots with high species richness and endemism (Myers 1988, 1990; Myers *et al.* 2000). Myers *et al.* (2000) report that the Western Ghats and Sri Lanka contain 4,780 plant species, of which 2,180 (45.6%) are endemic to the region. Similarly, of 1,073 vertebrate

species recorded from the region, 355 (33.1%) are endemic. The *ecoregion representation approach*, which also incorporates the preservation of distinct ecosystems and ecological processes in assigning conservation priorities, includes two ecoregions from the Western Ghats (Olson and Dinerstein 1998). These are the moist forests under terrestrial ecoregions and the rivers and streams under the freshwater ecoregions. The conservation status of the moist forests is considered to be critical or endangered (Olson and Dinerstein 1998). The freshwater ecoregions are threatened by damming, siltation, introduction of exotic species of fish, and pollution.

Moist forests, including tropical wet evergreen rainforest, are found largely south of 16° N, particularly south of the Palghat Gap in the southern Western Ghats. This is also the region that contains higher diversity and a greater number of endemics of rainforest plant and animal taxa (Nair and Daniel 1986, Daniels 1992, Vasudevan *et al.* 2001, Ishwar *et al.* 2001, Ali 1935, Ali 1936a-d, Ali 1937a-c, Ali and Ripley 1983, for birds see Section 2.1.7). This pattern is also evident in mammals, where species such as the Nilgiri tahr (*Hemitragus hylocrius*), Nilgiri langur (*Trachypithecus johnii*), and brown palm civet (*Paradoxurus jerdoni*), are confined largely to the southern portion of the Western Ghats (south of 13° 45' N, Kumar *et al.* 1999, Mudappa 2001).

2.1.4 Climate

The Western Ghats has a tropical climate that shows pronounced variation along north-south, east-west, and altitudinal gradients. Although, the region receives an average annual rainfall of 2,500 mm, this may vary depending on locality by an order of magnitude from less than 500 mm (in the eastern rain-shadow areas) to nearly 7,500 mm (on the western aspect). The distribution of rainfall across the year also varies from south to north. The southern end of the Ghats has a short dry season (2 – 5 months) as it receives rain from the southwest (June – September) and northeast (October – January) monsoons. The northern reaches have a longer dry season (5 – 8 months), receiving rain mostly during the southwest monsoon. The average annual rainfall in the evergreen forests ranges from around 2,000 to 7,500 mm depending on the locality (Pascal 1988, Daniels 1992).

Temperatures average 20° C in the south and 24° C in the north (Nair and Daniel 1986). The annual mean temperature varies from around 29° C at sea level to around 15° C at 2,400 m altitude. The change in mean temperature with elevation is gradually sigmoidal, with steeper rate of change occurring only in the mid-elevations between 400 m and 1,500 m, where there is a 0.8° - 0.9° C decrease per 100 m gain in altitude (Pascal 1988). Only the higher hills, which tend to have a subtropical climate, experience temperatures below 15° C and frost. Temperatures are often lower during the monsoon months (periods of high rainfall, Pascal 1988). Mist is frequent, particularly above 1,000 m altitude during the monsoons. The southwest monsoon season is characterised by heavy thundershowers punctuated by clear days and strong winds, the latter causing much uprooting of vegetation through tree falls. Heavy rainfall during the northeast monsoon is largely precipitated as

a consequence of cyclonic storms forming around atmospheric depressions in the Bay of Bengal. Exposed and leeward slopes also face moderate drying effects due to wind.

2.1.5 Vegetation

The pronounced north-south, east-west, and elevational gradients in climate have profound consequences for the distribution of plants and animals. The vegetation becomes drier as one progresses from west to east (rain shadow) across the hills. Lower elevations on the eastern aspect, receiving less than 1,200 mm annual rainfall contain tropical dry deciduous and thorn forest, with tropical moist deciduous forests in more well-watered areas (Champion and Seth 1968). With increasing elevation, tropical wet evergreen rainforest appears along the higher slopes and ridges. The western aspect of the hills tends to have mostly tropical moist deciduous and wet evergreen forest types at lower elevations, giving way to the latter type as one climbs higher. Above 1,800 m the evergreen forest becomes a unique, stunted montane formation called *shola*, that alternates with natural high altitude grasslands. The shola-grassland ecosystem is characteristic of the higher reaches of the Nilgiri, Palni, and Anamalai hills, in particular.

Pascal (1988) has classified the tropical wet evergreen forests of the Western Ghats into low (mostly below < 700 m), medium- (700 - 1,400 m), and high-elevation (> 1,400 m) types. These wet evergreen forest types are also referred to as tropical rainforests in this thesis. The wet evergreen forests of the plains and low elevations are characterised by the occurrence of dipterocarps such as *Dipterocarpus indicus, D. bourdillonii*, and *Vateria indica*. Other characteristic species include *Hopea parviflora, Kingiodendron pinnatum, Humboldtia brunonis,* and *Poeciloneuron indicum*. At least four types of medium-elevation wet-evergreen forests are recognised by Pascal (1988), and the bulk of the work in this thesis was carried out in the *Cullenia exarillata-Mesua ferrea-Palaquium ellipticum* type. Among the various wet evergreen forest types in the Western Ghats, the *Cullenia-Mesua-Palaquium* type is the one with the highest plant endemism (43.4%, Pascal 1988). This evergreen forest type occurs chiefly south of 12˚ N (limit of *Cullenia* distribution). This type has a lower elevational limit of 600 - 700 m and extends up to about 1,400 m. After a transition zone between 1,400 m and 1,600 m, this type is replaced by the *Schefflera spp.-Meliosma arnottiana-Gordonia obtusa* high elevation wet evergreen forest type and montane *shola* (Pascal 1988).

The remarkable diversity of habitat types in the Indian Peninsula, particularly due to the Western Ghats, has endowed it with an impressive diversity of plants. As Gamble (1935) notes: “The Presidency of Madras presents, probably, a more varied flora than any other tract of equal area in India, possibly in the world. This phenomenon is due to the combined effects of its geographical situation and its topography…The most interesting feature, and one that distinguishes it from the rest of the Indian Peninsula, is found in the dense, evergreen forests of the West and South with their wealth of sub-tropical species”.

Over 4,000 plant species are known from the Western Ghats, of which around 1,500 species (c. 35%) are endemic to this region (Nair and Daniel 1986). Kumar *et al.* (1999) report that of the 490 tree species found in low- and mid-elevation forests, 308 species (63%) in 58 genera are endemic, with 42 of these being monotypic. Plant genera that are highly speciose and contain a large proportion of endemics include: the dipterocarps *Dipterocarpus* (92% of 13 species), the cane palms *Calamus* (92% of 25 species), and the balsams *Impatiens* (86% of nearly 90 species). Similarly 60% of the Ebenaceae (20 species) and all leguminous trees (12 species) are endemic (Kumar *et al.* 1999).

Other characteristic features of the wet evergreen rainforests of the Western Ghats include the occurrence of an endemic conifer, *Podocarpus wallichianus*, the only conifer found in the peninsula. Two species of tree composites also occur, *Vernonia monosis* and *V. travancorica*. The latter species is restricted to the southern Western Ghats as are many other tree species such as *Gluta travancorica, Hopea utilis, Semecarpus travancorica, Garcinia travancorica, G. rubro-echinata, Goniothalamus wightii, Diospyros barberi* and *D. foliolosa,* and the palm *Bentinckia coddapanna* that prefers open steep slopes. The percentage of shrub, herb, and epiphyte species with such restricted distribution is even higher (Pascal 1988). On slopes and moderately disturbed areas in the wet evergreen rainforest zones, large tracts of a reed-like bamboo, mainly *Ochlandra travancorica, O. scriptoria,* and *O. beddomei*, all endemic to the Western Ghats, occur in dense tangles. There is also a great number of species of the so-called lower plants, including mosses and ferns. Among ferns are the huge tree ferns (*Cyathea spp.*) that are often seen along rainforest streams.

2.1.6 Fauna

Animal groups too are characterised by high diversity and endemism, particularly among the lower vertebrates. Nearly 10% (245 species) of the fishes found in India occur in the Western Ghats, of which 42% are endemic (Kumar *et al.* 1999). Of the 215 species of amphibians known from India, at least 120 are now known from the Western Ghats. Nearly three-fourths of these 120 species are typically found in tropical rainforests (Johnsingh 2001). Two groups of amphibians are prominent for their high degree of endemism: the limbless caecilians (14 species of the 17 known from India, Bhatta 1998) and rhacophorid tree frogs (83%). Among reptiles, around 480 species are known from India, of which 197 are known from the Western Ghats. Notable endemism is seen among the burrowing urolpeltid snakes (32 species in Western Ghats), which are confined almost entirely to the Western Ghats and Sri Lanka. Mammalian diversity is relatively low in the Western Ghats. Of the 400 species of Indian mammals, approximately 125 species are known from the Western Ghats. Twelve species, including 2 genera, *Latidens* (bat) and *Platacanthomys* (rodent), are unique to the Western Ghats (Kumar *et al.* 1999, Mudappa *et al.* 2001).

2.1.7 Birds of the Western Ghats

The avifauna of the Western Ghats includes a little over 500 bird species (Ali and Ripley 1983). A comprehensive recent review of the diversity, natural history, and biogeography of the Western Ghats avifauna is available in the work of Daniels (1989, 1997) and only some salient aspects are mentioned here. In this thesis, I follow the taxonomy and nomenclature of Indian birds of Inskipp *et al.* (1996) and Grimmett *et al.* (1998). Where bird species are referred to only by their English names, scientific names are available in Appendix 1.

Of the 507 bird species reported from the Western Ghats, about 360 species are terrestrial (Daniels *et al.* 1992, Daniels 1997). A large part of the diversity consists of widespread species that typically occur in the dry and moist deciduous forests and dry thorn forests. The tropical evergreen forests contain fewer species but a greater proportion of endemic and restricted-range species than similar rainforests in northeastern India (Ali and Ripley 1983, Daniels *et al.* 1992). Moist forests, particularly tropical evergreen rainforest in the southern Western Ghats, is a major habitat for about 100 species of birds, including 14 endemic species (Malabar Parakeet, Nilgiri Wood Pigeon, Malabar Grey Hornbill, Grey-headed Bulbul, White-bellied Treepie, Wynaad Laughingthrush, Grey-breasted Laughingthrush, Nilgiri Laughingthrush, Rufous Babbler, Black-and-Orange Flycatcher, Nilgiri Flycatcher, White-bellied Blue Flycatcher, White-bellied Shortwing, Crimson-backed Sunbird). Two other restricted range-species that occur in high-altitude grasslands in this region are the Nilgiri Pipit and Broad-tailed Grassbird). In all, there are 16 endemic birds in the Western Ghats. Of these, six species that are mostly montane forest birds (Wynaad Laughingthrush, Nilgiri Laughingthrush *Garrulax cachinnans*, Black-and-Orange Flycatcher, Nilgiri Flycatcher, White-bellied Shortwing, Nilgiri Pipit) are restricted largely to the Western Ghats south from southern Karnataka, where the higher hills are located.

A number of other bird species whose range is largely restricted to the Western Ghats and other mountain ranges in the Indian Peninsula, Sri Lanka, or the Himalaya, also occur in these tropical rainforests: e.g., Malabar Trogon, White-bellied Woodpecker, Great Hornbill, Asian Fairy Bluebird, White-cheeked Barbet, Mountain Imperial Pigeon, Rufous-bellied Eagle, Oriental Bay Owl, Jerdon's Baza, Black Baza, and Sri Lanka Frogmouth, the last two being considered near-threatened species (Collar *et al.* 1994). A total of 222 bird species, including 12 Western Ghats endemics, had been reported earlier from the Anamalai (Stonor 1946, Kannan 1998), and a further 14 species were recorded during this study including the endemic White-bellied Shortwing (Appendix 1).

The conservation status of the birds of the Western Ghats rainforests is poorly known. Only the hornbills receive protection under Schedule I of the Indian Wildlife Protection Act of 1972 (Anonymous 1994), although the conservation status of many other species may be equally serious or endangered. The 16 species of restricted-range birds in the Western Ghats include 12 of near-threatened conservation status (Stattersfield *et al.* 1998). A recent assessment reports that the Western

Ghats supports populations of one endangered species (Nilgiri Laughingthrush), three vulnerable species (Nilgiri Wood Pigeon, White-bellied Shortwing, Broadtailed Grassbird), and seven near-threatened bird species (Grey-headed Fish Eagle, Malabar Pied Hornbill, Great Hornbill, Nilgiri Pipit, Grey-breasted Laughingthrush, Black-and-Orange Flycatcher, Nilgiri Flycatcher), of which all but two inhabit chiefly tropical rainforests (BirdLife International 2001).

2.1.8 Land use, human impact, and loss of forests

The influence of humans as hunter-gatherers probably began to be felt in the Western Ghats during the Old Stone Age of the Palaeolithic over 12,000 years before the present (BP, Chandran 1997). Following this, during the Mesolithic (up to 5,000 years BP), humans began the transition to food cultivators, which elaborated and coupled with the development of pastoralism during the Neolithic (5,000 to 3,000 years BP). The conversion of primary tropical rainforests of the Western Ghats to more open secondary habitats is likely to have commenced about this time (c. 3,500 years BP) as indicated by changes in palynological samples (Chandran 1997). Little is recorded in early history about humans in the Western Ghats. Sastri (1975) quotes Pliny the Elder (c. 75 A. D.), the author of *Periplus of the Erythraean Sea*, describing the trade between the ancient Roman Empire and India: "They send large ships to these market towns [on the Kerala coast] on account of the great quantity and bulk of pepper and malabathrum [available there]." It is likely that pepper and malabathrum (cinnamon, *Cinnamomum malabathrum*) were cultivated, but they may have also been harvested from the evergreen forests, as they are to an extent even today. References to rice and millet cultivation in the hills of the Western Ghats are also made in the 2,000 year-old Tamil Sangam literature (Sastri 1975, Chandran 1997).

It is likely that in these early times, the main human influence on the Western Ghats forests involved the small-scale disturbances due to hunting, slash-and-burn cultivation, and extraction of forest produce practised by hill peoples. This is likely to have introduced deciduous elements and produced a mosaic of old-growth and secondary vegetation in evergreen forest areas (Chandran 1997). The most significant ecological changes occurred from the early 19th century onwards, following British colonisation and the ensuing exploitation of forests, although increasing populations and changing lifestyles, technologies, and needs also undoubtedly played a significant role in intensifying human impacts (Gadgil and Guha 1992).

Direct colonial impact on the evergreen forests was largely two-pronged: timber exploitation through forestry operations, and conversion to monoculture plantations of teak (*Tectona grandis*), tea (*Camellia sinensis*), coffee (*Coffea arabica*), wattle (*Acacia mearnsii*), *Eucalyptus*, and pine (*Pinus radiata*). Indirect influences included the penetration of remote areas through increased access by road. The temperate climate of the hills attracted the colonial rulers, where they established “settlements” to be used as summer stations. The landscape tranformations, which largely began in

earnest around the 1850s, grew and mushroomed well into the 20th century, continuing even after India's independence in 1947 (Gadgil and Guha 1992). The creation of reservoirs for hydroelectricity and irrigation in recent times has also submerged large areas of tropical forest in the Western Ghats.

Although estimates of forest areas that have been lost or converted in the Western Ghats vary, the figures are startling. Of the 62,000 km² of potential area of evergreen forests in the Western Ghats, Gadgil and Meher-Homji (1986) estimated that only between 5,288 km² (8.5%) and 21,515 km² (34.7%) remained in the mid 1980s along the ranges. A more recent assessment paints a bleaker picture. Myers *et al.* (2000) estimate that of the 182,500 km² of primary vegetation that was estimated to have existed in the Western Ghats and Sri Lanka, only some 12,450 km² (6.8%) remain today.

Within the state of Kerala alone, Chattopadhyay (1985) estimated that natural vegetation cover declined from 44% in 1905 to 17% in 1973. He also estimated that with a high deforestation rate of over 5% annually between 1973 and 1984, only 9-10% of the State's area remained under natural vegetation cover. On a wider scale, the Ministry of Environment and Forests of India estimated a decrease in forest cover in the five Western Ghats states (Maharashtra, Goa, Karnataka, Kerala, Tamil Nadu) by 20% between 1972-1982 and by a further 4.32% between 1982-1990, followed by an increase in 1992-3 (Ministry of Environment and Forests 1989, 1992, 1993). Menon and Bawa (1997) estimated that, between 1920 and 1990, 40% of the original natural vegetation of the Western Ghats was lost or converted to open/cultivated lands, coffee plantations, tea plantations, and hydroelectric reservoirs. Open/cultivated lands accounted for 76% and coffee plantations for 16% of the conversion. It must be noted that large-scale conversion to tea and coffee plantations had already occurred in many areas prior to 1920 (Congreve 1942, Prabhakar and Gadgil 1995).

The area under plantations is also large and growing today. Tea plantations in the south Indian states increased in area from 74,765 ha in 1987 to 87,993 ha in 1998. In 1998, over 195,000 people were employed in this US$ 400 million (c. Rupees 18 billion) industry (1999 Statistics of the Tea Board of India). Large areas of *Eucalyptus*, used as fuelwood for the factories, also occur with tea. Similarly, in 1999–2000, the US$ 500 million (c. Rupees 22.5 billion) Indian coffee industry had 293,000 ha of plantations, almost entirely in southern India. This industry, employing over 520,000 people and producing over 170,000 tons of coffee annually, accounts for substantial non-natural forest canopy cover in the states of Karnataka, Kerala, and Tamil Nadu in the Western Ghats (Coffee Board Statistics 2001).

In recent decades, increasing development, human impact, and the spread of plantations, particularly tea, coffee, and *Eucalyptus*, have been responsible not only for forest loss but are also major causes of forest fragmentation in the Western Ghats. Menon and Bawa (1997) estimate that between 1920 and 1990, the number of forest patches have increased four-fold, while the average size of these patches has declined by 83%. Evergreen forests have borne the brunt of these impacts. In addition to direct loss, conversion, or fragmentation, evergreen forests today also face degradation to more open, deciduous, or secondary vegetation due to chronic human extraction of forest products

(Daniels *et al.* 1995). The gradual replacement of climax and endemic evergreen plant species by pioneer, heliophilic, widespread, and common species by such human impact is a matter of conservation concern (Daniels *et al.* 1995).

Factors that have worked against the loss and denudation of natural forest cover include both local and state-sponsored efforts at forest conservation. Local human communities in many parts of the Western Ghats have traditionally protected small patches of forests as sacred groves, a large number of which exist even today in states such as Maharashtra, Karnataka, and Kerala (Chandran *et al.* 1998). The conservation value of such forest remnants is increasingly being recognised in recent times (Gadgil and Guha 1992, Turner and Corlett 1996, Laurance and Bierregaard 1997). In addition, substantial areas have been included within the system of Protected Areas established under India's Wildlife Protection Act of 1972. These conservation areas are, however, far from being completely secure. Sacred groves face degradation with the waning influence of traditional values and the stronger forces of modern markets and lifestyles. Forests within and around Protected Areas face the continual effects of human extraction of forest products (Daniels *et al.* 1995), hunting of wildlife species (Madhusudan and Karanth 2000), and fragmentation (Kumar *et al.* 1995, Umapathy and Kumar 2000) all along the Western Ghats.

There is thus an urgent need to study the effects of habitat alteration on native species of the Western Ghats. In addition, the conservation value of secondary habitats and plantations needs to be evaluated. Coffee plantations with a canopy of shade trees, in particular, abut many Protected Areas in the Western Ghats and are used by a variety of animals. Given their location and areal coverage, these habitats need to be evaluated for the species they support and their role in maintaining communities in present-day landscapes.

2.2 THE KALAKAD-MUNDANTHURAI TIGER RESERVE

A major part of this study (Chapters 3 - 5) was carried out in the Kalakad-Mundathurai Tiger Reserve (KMTR) in Tamil Nadu. KMTR, along with the other sanctuaries lying across the administrative boundary in Kerala state (Neyyar, Peppara, and Shendurni), forms a tract of forest ranging over 1,500 km² in the Agastyamalai-Ashambu hill range. This makes it one of the most significant areas for conservation of biological diversity in the Western Ghats (Johnsingh 2001). In the Western Ghats, KMTR and adjoining areas have one of the largest and last remaining contiguous tracts (over 400 km²) of tropical rainforest (Plate 1, Ramesh *et al.* 1997). As most of this area has not been logged or converted to plantations like in other parts of the Western Ghats, the primary rainforest vegetation in KMTR offers a unique opportunity to study patterns of distribution of animal taxa across natural gradients in a relatively undisturbed setting (Ishwar *et al.* 2001, Mudappa *et al.* 2001, Vasudevan *et al.* 2001). Past research in KMTR has been reviewed by Johnsingh (2001). Studies on birds in KMTR have been restricted to the drier forests on the Mundanthurai plateau (communities: Joshua and

Johnsingh 1988, Johnsingh and Joshua 1994; ecology of migrant Greenish Leaf Warbler: Katti 1997, Katti and Price 1996, 1999). Ganesh (1995) and Ganesh and Davidar (1999) studied the patterns of fruiting phenology and fruit use by vertebrates, including frugivorous birds, in Kakachi. The rainforest bird community structure has not been studied earlier.

2.2.1 Location and extent

KMTR is an 895 km² sanctuary located between 8° 25' to 8° 53' N and 77°10' to 77°35' E at the southern end of the Western Ghats, in Tirunelveli and Kanyakumari districts of Tamil Nadu state (Figure 2.2). The Reserve ranges from about 50 to 1,700 m above mean sea level in elevation, with rainforests occurring chiefly above 500 m. The topography is rugged with numerous perennial hill streams originating from the tropical rainforest areas on the upper slopes and joining to form major rivers such as the Tambiraparani, Manimuthar, and Ramanadhi, which support the agricultural economy of millions in the adjoining plains.

The fieldwork in this study was carried out from three base camps located within the extensive rainforest tract in KMTR (Figure 2.3). The major base was the field station at Sengaltheri (8° 31' 15" N and 77° 26' 52" E, altitude: 1,040 m). Low-elevation areas were accessed from Kannikatti (8° 37' N and 77° 16' E, altitude: 770 m), whereas mid- and high-elevations were surveyed from the base camp at the Fern House in Kakachi (8° 50' N and 77° 30' E, altitude: 1,250 m).

2.2.2 Vegetation

The rainforest vegetation in KMTR has been classified as tropical wet evergreen forest (Tirunelveli hill top forest, Champion and Seth 1968). It has also been categorised as mid-elevation tropical wet evergreen rainforest of the *Cullenia exarillata-Mesua ferrea-Palaquium ellipticum* type (Pascal 1988). KMTR is believed to contain at least 2,000 (or over 50%) of the plant species found in the Western Ghats, a significant part of which occurs in the wet evergreen rainforests (Ganesh *et al.* 1996). Physiognomically, the forest is dominated by dense woody vegetation and has a tall stature with emergents reaching up to around 40 m, at lower and mid-elevations. The average canopy height is around 25 m and with a high canopy closure (cover) of around 95%. Canes and lianas are common. Floristically the vegetation is unique, containing around 150 localized plant endemics.

The emergent trees of these rainforests include species such as *Cullenia exarillata, Palaquium ellipticum,* and *Elaeocarpus tuberculatus*. The canopy typically contains *Mesua ferrea,* species of *Litsea* and *Cryptocaria* and other Lauraceae*, Diospyros sylvatica, Canarium strictum, Mangifera indica, Myristica dactyloides, Scolopia crenata, Filicium decipiens, Dimocarpus longan, Artocarpus heterophyllus, Cinnamomum malabathrum,* and *Holigarna nigra*. Trees and shrubs of the lower storeys include *Agrostistachys borneensis, Antidesma menasu, Nothopegia beddomei, Gomphandra*

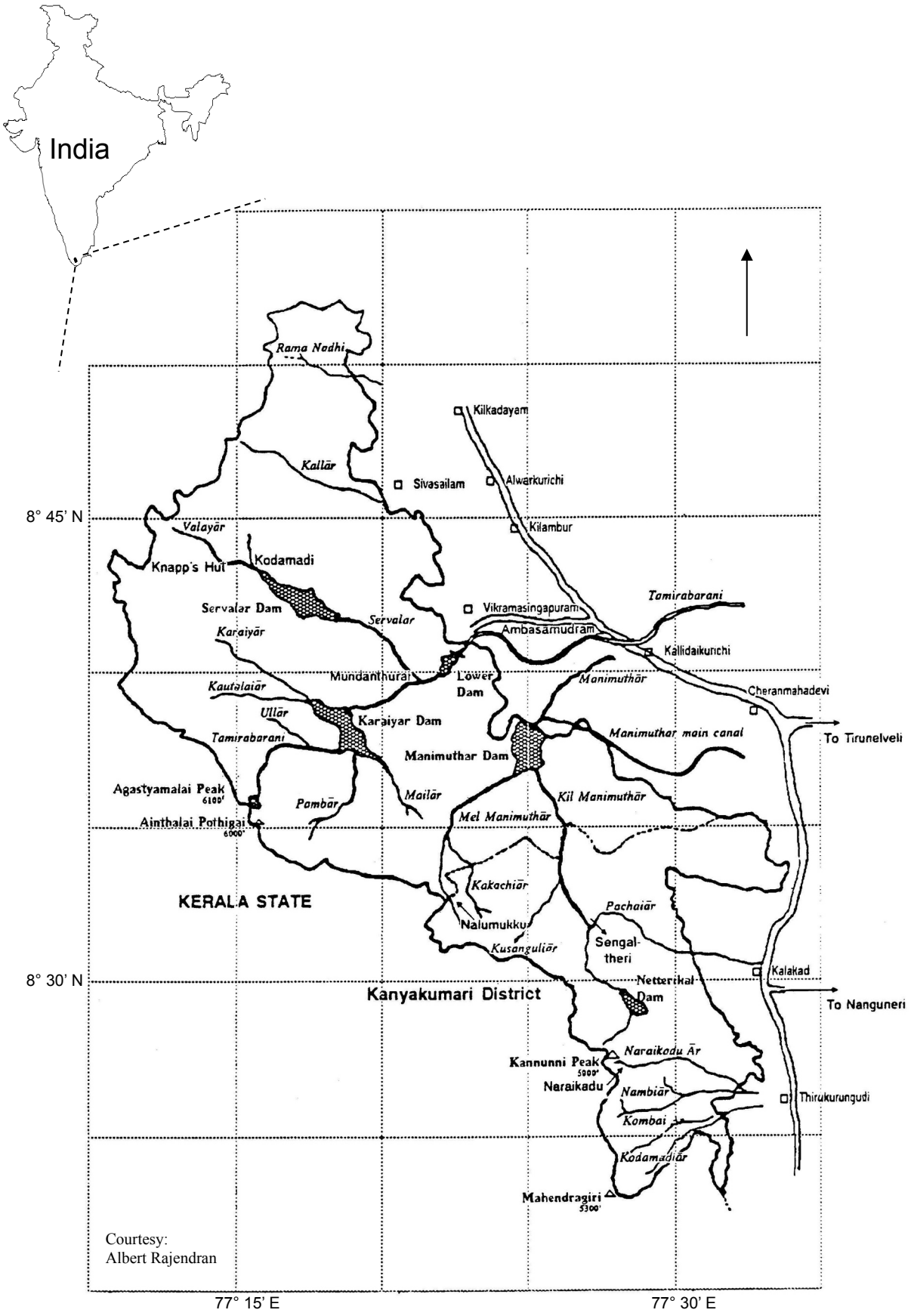

Figure 2.2: Map of the Kalakad-Mundanthurai Tiger Reserve showing major localities and rivers.

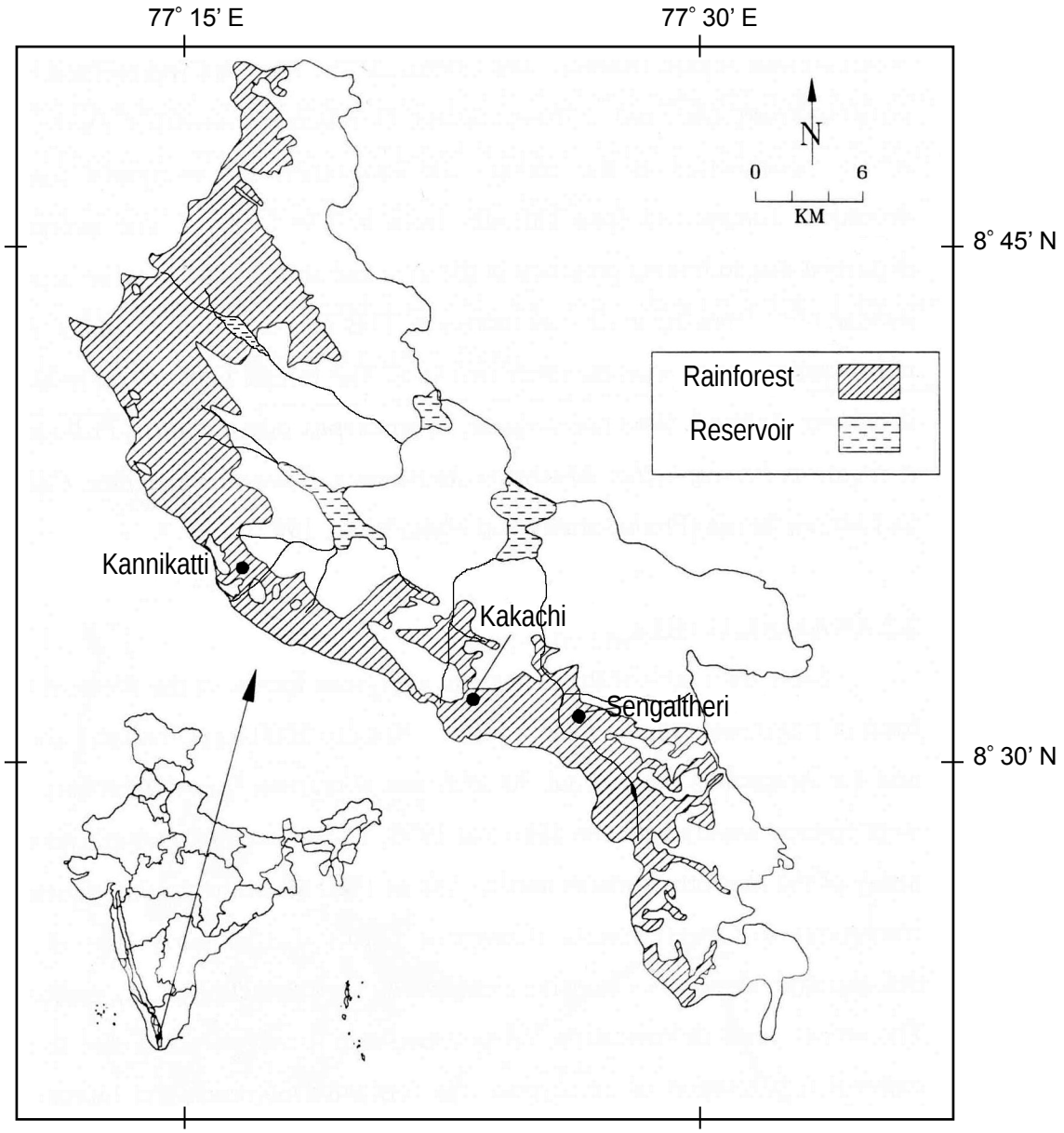

Figure 2.3: Map of the Kalakad-Mundanthurai Tiger Reserve showing the three main base camps and distribution of tropical rainforest

coriacea, Isonandra lanceolata, Apollonias arnottii, Psychotria spp., Mallotus stenanthus, Eugenia spp., Lasianthus cinereus, Saprosma corymbosum, and *Saccandra chloranthoides.* In disturbed edges, species such as *Macaranga peltata, Clerodendrum viscosum, Leea indica, Trema orientalis,* and the stinging elephant nettle *Dendrocnide sinuata* occur. Among the climbers and lianas, several species of canes (*Calamus spp.*) occur along with *Piper nigrum, Diploclisia glaucescens, Strychnos colubrina, Canthium angustifolium, Elaeagnus kologa,* and the gymnosperm *Gnetum ula*. Detailed descriptions of rainforest vegetation are available elsewhere (Ganesh *et al.* 1996, Krishnan and Davidar 1996, Parthasarathy 1999, 2001).

2.2.3 Climate

Within the rainforest, the mean monthly daytime temperature (average of mean daily maximum and mean daily minimum calculated across all days in the month) ranges between 19° C in January and 24° C in April–May (at Sengaltheri, 1,040 m). The lowest temperature recorded in any day in Sengaltheri was 15° C (January 1998) whereas the maximum was 31° C (June 1998). The average annual rainfall is over 2,200 mm. The total rainfall was 2,283 mm in 1998 and 2,230 mm in 1999 at Sengaltheri (Figure 2.4). There are three seasons: (a) dry season (February to May), (b) southwest or summer monsoon (June to September), and (c) northeast or winter monsoon (October to January). Strong winds occur during the southwest monsoon, when periods of heavy rainfall often alternate with days of bright clear weather. KMTR receives over half its annual precipitation during the northeast monsoon. Elevations above 1,000 m experience frequent mists and cloud cover, which may be prolonged over days or even weeks during the northeast monsoon. The average relative humidity ranges from around 60% in March to over 90% in November and December.

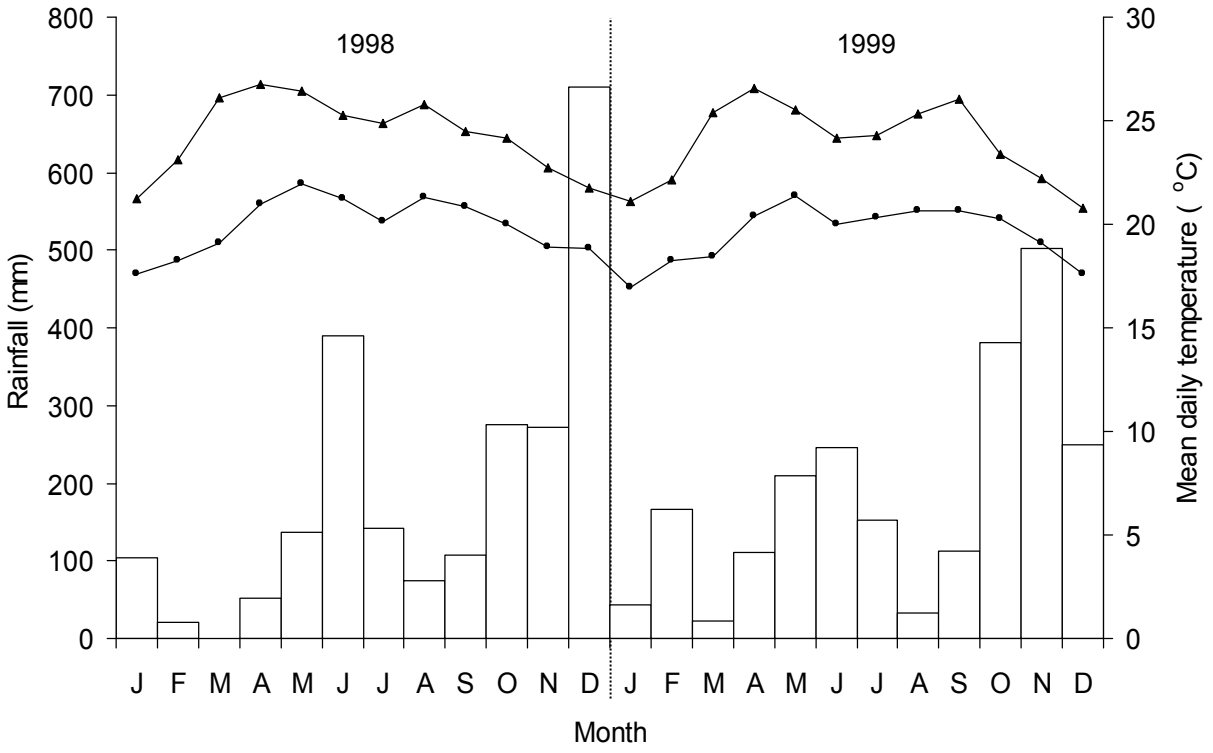

Figure 2.4: Monthly rainfall (bars) and mean daily minimum and maximum temperatures (lines) at Sengaltheri, Kalakad-Mundanthurai Tiger Reserve, 1998-1999.

2.2.4 Fauna

A total of 33 fish, 37 amphibian, 81 reptile, and 76 mammal species have been recorded from KMTR (Johnsingh 2001). The herpetofauna includes the recently rediscovered rainforest lizard *Calotes*

andamanensis and the microhylid frog *Melanobatrachus indicus* and is described in two recent studies from the area (Vasudevan 2000, Ishwar 2001, Ishwar *et al.* 2001, Vasudevan *et al.* 2001). Of the non-volant mammals, 8 species are endemic to the Western Ghats. The large carnivores include the tiger *Panthera tigris,* leopard *P. pardus*, dhole *Cuon alpinus*, and sloth bear *Melursus ursinus*. Eight species of small carnivores occur in the rainforests of KMTR (Mudappa 1998a). Other mammals occurring in the rainforest include the Asian elephant *Elephas maximus,* gaur *Bos gaurus*, sambar *Cervus unicolor*, mouse deer *Moschiola meminna*, lion-tailed macaque *Macaca silenus*, bonnet macaque *M. radiata*, Nilgiri langur *Trachypithecus johnii*, Nilgiri tahr *Hemitragus hylocrius*, Malabar giant squirrel *Ratufa indica*, large brown flying squirrel *Petaurista philippensis*, seven other species of rodents, and three species of shrews (D. Mudappa, personal communication). At least 17 bat species are known from KMTR (Johnsingh 2001).

Although 278 bird species have been recorded in and around KMTR, only 84 species occur in rainforests (Appendix 1). The remaining species occur mainly in drier forests, water bodies, and other habitats. This pattern of relatively low bird species richness in the rainforests is typical of other hill ranges in the Western Ghats (e.g. Anamalai hills, Kannan 1998) as well as the entire region (Daniels *et al.* 1992). This is due to the restricted area occupied by rainforests and their historical isolation from large tracts of rainforests in northeast India and southeast Asia. Similar areas of rainforest in northeast India tend to have nearly thrice the number of bird species (Ali 1977, Daniels *et al.* 1992). In the rainforest of KMTR, 13 species of winter migrants arrive around October and stay till April. Other rainforest species are resident year-round, and include 12 of the 15 species endemic to the Western Ghats. A majority of species breed between late January and May (Ali and Ripley 1983, T. R. S. Raman, personal observations).

2.2.5 Management, people, and land-use history

The Kalakad-Mundanthurai Tiger Reserve was notified as a Tiger Reserve in 1988-89 combining the pre-existing Mundanthurai Wildlife Sanctuary (567 km², constituted in 1962) and Kalakad Wildlife Sanctuary (250 km², constituted in 1976, Kant 1998). Besides these areas within Tirunelveli District, parts of Veerapuli and Kelamalai Reserve Forests of Kanyakumari district were added in 1996 (Melkani 2001). Of the total area of 895 km² today, 538 km² is in the core zone, 324 km² in the buffer zone, and 35 km² in a tourism zone (Mundanthurai and Thalayanai). Fortunately, the entire area of the remarkable tropical rainforest of this region is included within the core area.

In the past, land-use within the reserve was limited, going by available records (Kant 1998). Between 1888 and 1915, contractors operated within the area to extract and sell forest produce such as cane, honey, and spices. This continued in Mundanthurai range up to 1980. A Kani (local tribe) cooperative was formed at this time. Minor forest produce extraction continued till 1984. In Kannikatti area and in Kodamadi, light selection felling was carried out from 1927 for *Mesua* sp.

Coupes were worked to supply sleepers and hut-construction materials to the British armed forces between 1942-43. The felling is reported to have been heavy until a ban was imposed in the Tambiraparani, Servalar, and Manimuthar catchment. Teak and softwood plantations were established (in areas such as Mundanthurai and Thalayanai) from 1917 onwards (Kant 1998).

An area of 5,605 ha of plantations have been established within KMTR over the years (Ali and Pai 2001). The largest area (3,391 ha) is within the leased property of the Bombay Burmah Trading Corporation, containing mainly tea plantations, but with some cardamom and *Eucalytptus*, adjoining the tropical rainforests of Kodayar and Kakachi. The lease on this area will expire in 2028. A labour force of about 6,600 people work on this estate in the Manjolai area. The second largest area is the Kattalamalai estate (1,271 ha), bordering low-elevation rainforest areas in Kannikatti, and planted with coconut (*Cocos nucifera*) and *Eucalyptus*. Of the 54.86 ha of cardamom plantations reported in Kant (1998), 34.62 ha were leased out in Mundanthurai range (Walayar) and the lease expired in 1998-99. The lease on the remaining 20.24 ha in Kalakad range in Sengaltheri expired in 1995, after which it was abandoned. These, along with an abandoned cardamom plantation near Kakachi set aside by the BBTC as part of a forest corridor, were sampled during this study.

Ali and Pai (2001) give further details about the enclaves within KMTR including leased areas, *patta* lands, abandoned estates, religious enclaves, and electricity board settlements adjoining the lower and upper Papanasam, Servalar, and Kodayar dams. In 1991, 106 tribal (mostly Kani) families lived in five settlements within KMTR: Agasthiar Nagar, Servalar, Chinna Mylar, Periya Mylar, and Injikuli, the last named being close to low-elevation rainforest in Kannikatti (Kant 1998). The plains around KMTR are densely populated and about 145 villages containing about 30,000 households are found within 5 km of the eastern boundary. These people, particularly those who graze their livestock within KMTR or extract forest produce and fuelwood, have been the targets of a large ecodevelopment programme worth Rs. 91 million (c. US$ 2 million) since 1995 (Melkani 2001). Most of their impact is on the dry deciduous and dry thorn forests along the eastern boundary.

2.3 THE ANAMALAI HILLS

The final phase of this study (Chapter 6) was carried out in the Anamalai (which in Tamil means the elephant hills) ranges, a major conservation area in the southern Western Ghats. The ranges occur just south of the Palghat gap and are linked with the Nelliampathy hills towards the west, the Palni hills toward the southeast, and the Eravikulam, High Wavy and other ranges towards the south. A number of Protected Areas span this region, including the Indira Gandhi Wildlife Sanctuary (WLS, 987 km²) in the Anamalai hills, Eravikulam WLS (97 km²), Chinnar WLS (90 km²), Parambikulam WLS (274 km²), reserve forests, and the new Kodaikanal WLS in the Palni hills (Figure 2.5). Thus the Anamalai hills, like the Agasthyamalai hills, covers a large forested region of great significance for conservation in the Western Ghats.

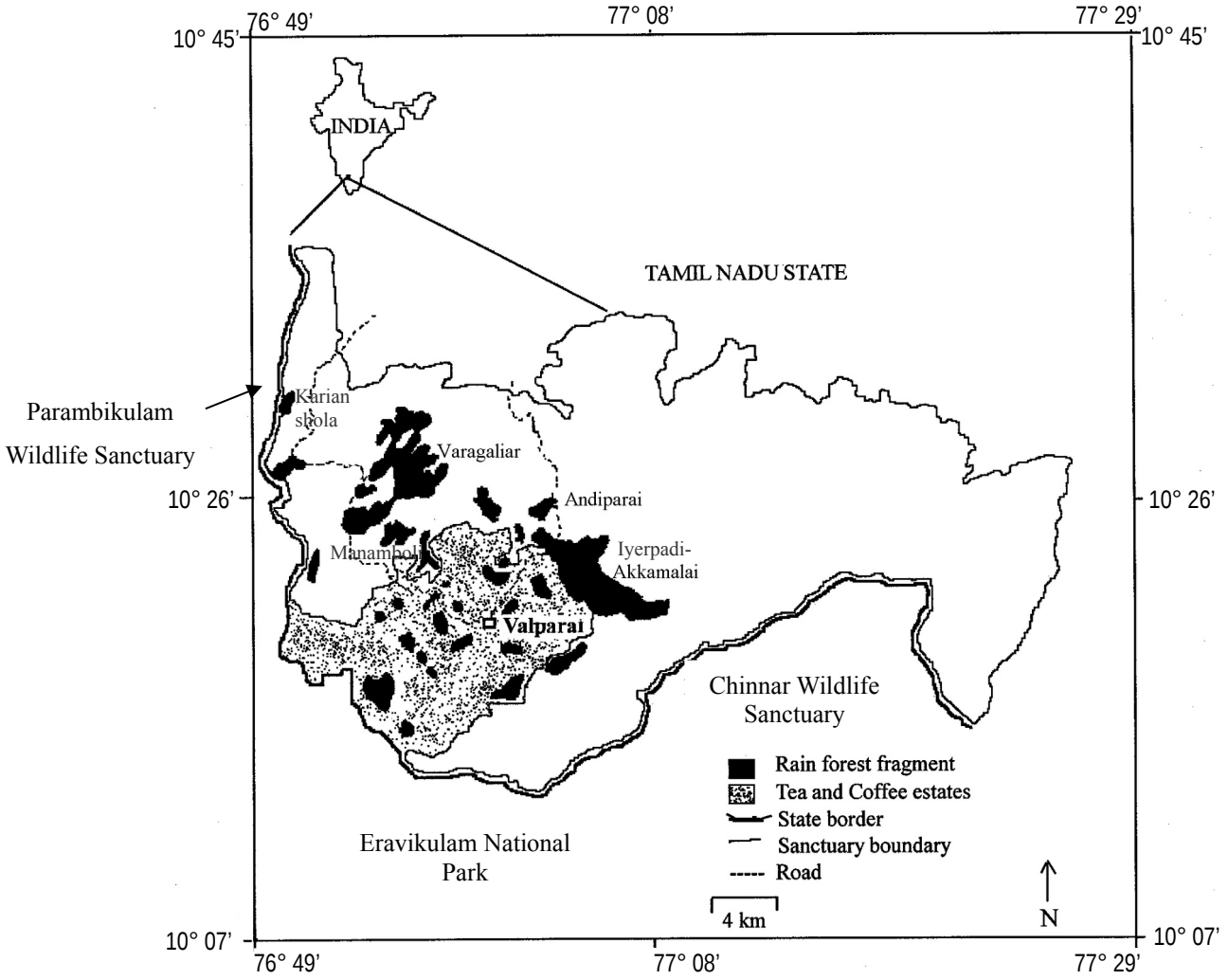

Figure 2.5: Outline map of the Indira Gandhi Wildlife Sanctuary indicating plantations and rainforest areas around Valparai and surrounding Proteced Areas.

However, in contrast to the Agathyamalai region, the mid-elevation tropical rainforests of the Anamalai have been severely fragmented over the last century due to large-scale conversion of rainforest into commercial plantations of tea, coffee, *Eucalyptus*, and cinchona (Plate 1). A number of recent studies have explored the effects of this large-scale habitat fragmentation on plant and animal taxa: butterflies (Babu 2000), amphibians (Vasudevan 2000), reptiles (Ishwar 2001), and mammals (Kumar *et al.* 1995, Singh *et al.* 1997, Prabhakar 1998, Kumar 2000, Kumara *et al.* 2000, Rajamani 2000, Umapathy and Kumar 2000, Mudappa 2001). The effects on birds of fragmentation and conversion to plantations has not been studied earlier.

2.3.1 Location and extent

The Indira Gandhi Wildlife Sanctuary earlier known as the Anamalai Wildlife Sanctuary (987 km², 10° 12' N to 10° 35' N and 76° 49' E to 77° 24' E) lies almost centrally amidst the above-mentioned Protected Areas in the Anamalai hills. The altitude within the sanctuary ranges from 220 m in the

foothills along the northern fringes to 2,513 m atop Thanakkanmalai in the Grass Hills at the southern portion of the reserve. The region is drained by perennial rivers such as the Konalar, Varagaliar, Karuneerar, Chinnar, and Amaravathi. A number of reservoirs (Aliyar, Upper Aliyar, Kadamparai, Upper and Lower Nirar, Thirumurthy, and Parambikulam, range at least partly into the Indira Gandhi Wildlife Sanctuary.

Although a large area of tropical rainforest occurs within the sanctuary, much of it occurs as fragments on private lands on the Valparai plateau. The Valparai plateau containing plantations, estates, and fragments lies centrally amidst the conservation areas mentioned earlier. The topography on the plateau is undulating, occasionally rising into minor peaks, and ranging in altitude from 900 m to 1,500 m. At least 25 rainforest fragments, including 14 on private lands occupying a total of over 320 ha have been identified so far in and around this area (Kumar *et al.* 1995, Umapathy and Kumar 2000). Additional sites do exist and a thorough survey and mapping is yet to be carried out. The plantations and fragments are surrounded on all sides by Protected Areas that contain significant wildlife populations. Many species move through this fragmented landscape between conservation areas, including large mammals such as Asian elephant, tiger, leopard, and dhole, and birds such as Great Hornbills. The conservation of rainforest fragments has also been highlighted as being important as corridors for these wide-ranging taxa (Kumar 2000).

2.3.2 Climate, vegetation, and fauna

The climate of the Anamalai hills is similar to the Agasthyamalai region. As the Western Ghats are nearly at their widest in this region, there is considerable variation from west to east. The western windward slopes and upper reaches receive around 3,500 mm (up to around 5,000 mm) of rain annually and typically contain tropical wet evergreen forests. The extreme eastern parts have tropical dry deciduous forests, giving way to tropical dry thorn as the hills meet the plains—these areas may receive as little as 500 mm of rain annually. The total rainfall in Injipara on the Valparai plateau was 3,279 mm in 1998 and 2,895 mm in 1999. Like KMTR, this region receives rainfall during the southwest and northeast monsoons, but unlike KMTR over 70% of the precipitation occurs during the former season (average rainfall between 1989 - 1998 was 3,497 mm, distributed as in Figure 2.6).

In contrast to the other Protected Areas in the Anamalai hills, which contain large areas of tropical dry and moist deciduous forests, and high-altitude shola-grassland ecosystems, much of the key mid-elevation tropical evergreen forest of interest to this study occurs in the Indira Gandhi Wildlife Sanctuary and the Valparai plateau. Most of this rainforest falls within the classification of mid-elevation tropical evergreen forest of the *Cullenia-Mesua-Palaquium* type (Pascal 1988). Description of the evergreen forest vegetation around Varagaliar is provided by Ayyapan and Parthasarathy (1999) and Annaselvam and Parthasarathy (1999).

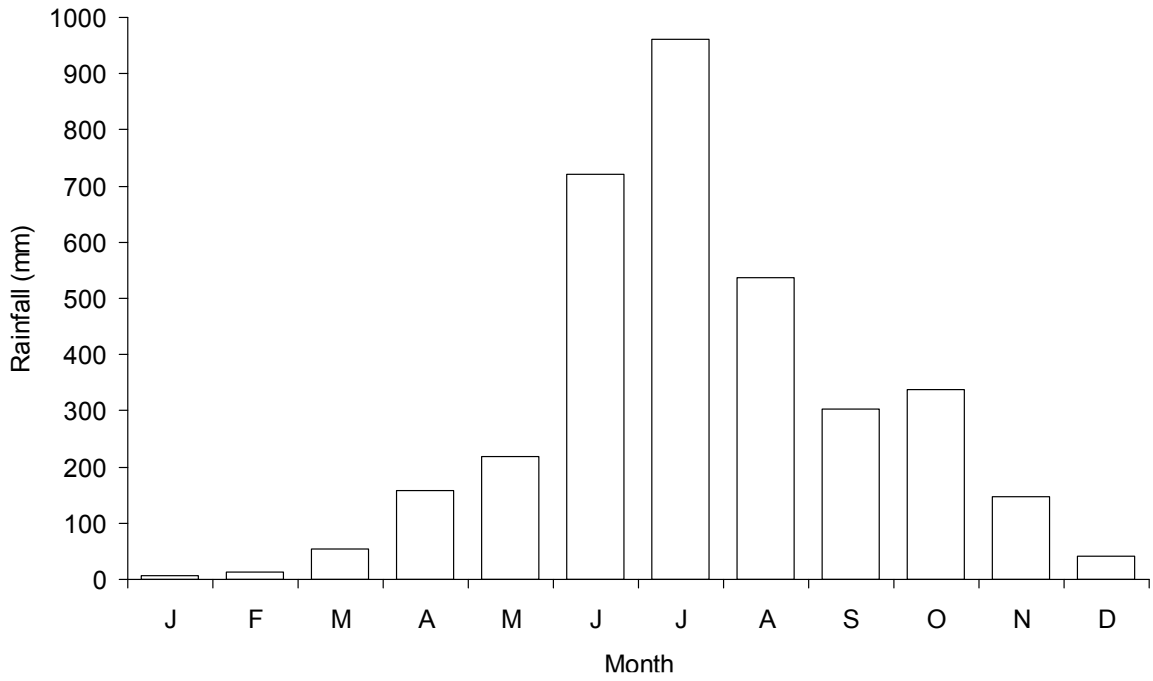

Figure 2.6: Mean monthly rainfall near Valparai in the Anamalai hills over a ten-year period between 1989-1998 (Data courtesy: Injipar

Although there are differences in the herpetofauna between the Anamalai and Agasthyamalai hills (Ishwar 2001, Vasudevan 2000), the mammal and bird fauna is largely similar in the two regions. Among mammals, notably, the barking deer (*Muntiacus muntjak*) is common here and there are sizable populations of Nilgiri tahr in the upper reaches. Between the two regions, only six typically low-elevation rainforest bird species have been recorded exclusively in the Anamalai hills so far−Heart-spotted Woodpecker, Dollarbird, Blue-bearded Bee-eater, Great Eared Nightjar, Spangled Drongo, and Blue-eared Kingfisher. Also, only three relatively rare bird species in rainforests have been recorded exclusively from KMTR so far—Oriental Dwarf Kingfisher, Brown Wood Owl, and Pied Thrush (Appendix 1). The remaining 82 species of rainforest birds, including 12 winter migrants, are known to occur in both study sites. Thus, in vegetation and fauna, the Anamalai hills is similar to the Agasthyamalai hills, at least when the same altitudes are compared. Notable bird studies from the Anamalai hills include studies on the ecology of the Great Hornbill (Kannan 1994) and the Malabar Grey Hornbill (Mudappa and Kannan 1997, Mudappa 2000). Accounts of the birds of the Anamalai hills have been given earlier by Stonor (1946) and Kannan (1998).

2.3.3 People and land-use history

During colonial times, the Anamalai hills was an important timber-extraction area. Extraction began around the 1830s and continued intensively until it declined around 1862-3 (Sundararaju 1987). Reservation of the forest tracts began from 1883. Logging continued in the northern part of the

sanctuary area until 1976. Tea and coffee estates burgeoned in the hills around the Valparai area from the mid 1800s. A coffee estate at Poonachi was recorded as existing as early as 1858. The Waterfall and Waverley estates were the earliest to be established on the Valparai plateau in 1864 (Congreve 1942). By 1900, the area under coffee, tea, and cardamom was 1,155 acres, 545 acres, and 843 acres, respectively. By 1916, this had increased to 2,256 acres under coffee, 6,912 acres under tea, 2,305 acres under cardamom, with an additional 1,844 acres under rubber and cinchona (Congreve 1942). Over a dozen estates had been established by 1930. The process continued even after independence. At the present day, the reserve contains 18,032 ha of tea, coffee, and cardamom estates and 3,717 ha of cinchona (half of which has been converted to tea, Sundararaju 1987).

The condition of the forests around 1897 can be judged from the following quote from Congreve (1942): "There were miles and miles of evergreen forest, with a few main paths running through it made by the huge herds of elephants which roamed there in the dry weather…The only inhabitants were a few Kaders living here and there in small communities, collecting minor forest produce, and making small clearings of hill rice, maize, and ragi, on which they largely lived. The only method of leaving the district was to walk to the foot of the hills, and then proceed by bullock cart to Coimbatore." Today, the situation is radically different. The Valparai plateau has only fragments of rainforest that are virtually islands surrounded by plantations of tea, coffee, and *Eucalyptus*. This area has a small town (Valparai) and a human population of over 200,000 people, including estate labourers, businessmen, government staff, and dependents, scattered across the town and the 54 estates around it. Indigenous tribal people, belonging to six main tribal communities (Kadars, Malasars, Malamalasars, Eravalars, Pulaiyars, and Muduvars) live within the area, scattered in many settlements (Sundararaju 1987). A good network of roads connects the settlements, factories, and estates. The main road from Pollachi to Chalakudi, busy with traffic, passes through many fragments on the Valparai plateau. A large number of people depend on the rainforests for fuelwood and many fragments have become noticeably degraded due to the chronic extraction. Removal of trees from fragments (e.g. removal of over 500 trees from Puthutotam estate in 1992) and conversion of shade-coffee estates to tea plantations are other forces of change inimical to conservation in the region.

CHAPTER 3

Assessment of census techniques for inter-specific comparisons and monitoring of tropical rainforest bird densities

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CHAPTER 3

Assessment of census techniques for inter-specific comparisons and monitoring of tropical rainforest bird densities

3.1 INTRODUCTION

Conservation monitoring programmes often target bird populations. If appropriate methods are used, birds are usually easy to identify and count in the field. In addition, there are often close linkages between birds and the structure and quality of their habitat. Monitoring bird populations in remnant natural and man-modified habitats can thus be used to track species declines and environmental changes (Furness and Greenwood 1993), and ultimately aid in bird conservation.

Among the principal techniques developed and used for censusing birds are transects, point counts, and territory mapping (Verner 1985, Bibby *et al.* 1992). Assessing which technique gives the most accurate population estimates is possible only when the actual population size is reliably known, such as by total mapping of banded individuals (Verner 1985). To select the best technique for a given objective, many studies have compared different methods to assess their relative accuracy, bias, precision, and convenience of application in the field (Ralph and Scott 1981, DeSante 1986, Verner and Ritter 1985). Such studies may also prove useful in comparing bird populations or relative abundance estimates collected using different methods in different sites or years.

In temperate regions, there has been extensive research, development, and standardisation of appropriate methods to census birds (Kendeigh 1944, Emlen 1977, Järvinen 1978, Reynolds *et al.* 1980, Ralph and Scott 1981, Taylor *et al.* 1985, Verner 1985, Hutto *et al.* 1986, Bibby *et al.* 1992, Gibbons *et al.* 1996). These have helped to develop monitoring programmes that have described long-term trends in bird populations, highlighted species in decline, and unravelled underlying causes

(O'Connor and Fuller 1985, Diehl 1985, Askins and Philbrick 1987, Terborgh 1989, James *et al.* 1996).

In contrast, little is known about population trends of tropical birds. Developing appropriate census methods for tropical bird populations is difficult due to the diversity of species and their social systems, patterns of migration and nomadism, and cryptic behaviour of many species (Karr 1981). Methods developed largely for use in the temperate region may need to be considerably modified for censusing tropical birds (Terborgh *et al.* 1992, Thiollay 1994, Robinson *et al.* 2000). Inter-specific comparisons of the consistency, accuracy, and precision of density or relative abundance estimates obtained by different methods are useful for community-level studies (Verner 1985, Wiens 1989). Such comparisons also help identify and standardise methods for monitoring tropical bird populations.

This chapter describes a comparative study of bird censusing techniques carried out in the tropical rainforests of the Western Ghats. This region is recognised as a global biodiversity hotspot (Myers *et al.* 2000), one of the 200 globally most important ecoregions (Olson and Dinerstein 1998), and an endemic bird area (Stattersfield *et al.* 1998). The Western Ghats has a long history of forest loss, conversion, and fragmentation due to logging, monoculture plantations, mining, and hydro-electric projects (Chattopadhyay 1985, Nair 1991, Chandran 1997, Menon and Bawa 1997). Although such human impact continues even today (Kumar *et al.* 1995, Daniels *et al.* 1995) with recognisable effects on avifauna (Daniels *et al.* 1990b), there has been little concerted effort at long-term monitoring of population trends of forest birds.

This study in an Asian tropical rainforest region is a first attempt to compare bird densities estimated using variable-width point and line transects (Buckland *et al.* 1993) with fixed-width estimators, territorial spot-mapping, and various abundance indices. The main objectives were to compare: (1) density estimates from variable-width line transects, variable-radius point counts, and territory spot-mapping, (2) simple fixed-width line transect and fixed-radius point count estimates with corresponding variable-width estimates, and (3) indirect and direct measures of relative abundance. The results are used to select methods with potential application for density estimation and conservation monitoring programmes involving both amateur and professional ornithologists.

3.2 STUDY SITE

The intensive study site and base camp were at Sengaltheri (1,040 m). in the Kalakad-Mundathurai Tiger Reserve (see Chapter 2). This area contains mid-elevation tropical rainforests ranging in altitude between 800 m to 1,250 m, and is contiguous with rainforests elsewhere in the Reserve. The terrain is rugged, mountainous, and dissected by many perennial streams. All bird sampling reported in this chapter was restricted to between 940 m and 1,140 m asl. The sites sampled are in undisturbed rainforests with tree and liana (> 20 cm girth at breast height) densities of over 900/ha, with a maximum canopy height of about 30 m. The sites have a dense undergrowth of shrubs, herbs, and

canes (*Calamus* sp.). The common canopy trees are *Mangifera indica, Syzigium spp., Filicium decipiens, Cullenia exarillata, Palaquium ellipticum, Mesua ferrea,* and *Cryptocarya bourdilloni*. Understorey trees include *Antidesma menasu, Epiprinus mallotiformis, Acronychia pedunculata, Eugenia sp.,* and *Nothopegia beddomei.* More details on vegetation are available in Parthasarathy (1999, 2001).

3.3 STUDY SPECIES

Bird taxonomy and names (see Table 1 for scientific names) follow Inskipp *et al.* (1996) and Grimmett *et al.* (1998). The thirteen most common resident bird species were selected for this study because only they had sufficient sample sizes for analysis by the different methods. Observations of behaviour and singing suggested that these birds appeared to possess conventional territories throughout the year (12 species) or at least during the breeding season (one species). Of the species studied, Crimson-backed Sunbird and White-bellied Blue Flycatcher, are endemic to rainforests of the Western Ghats. Nomadic species, long-distance migrants, and rarer species were excluded.

A summary of the diet-guild, habitat-niche, and basic social organisation (pair-forming, flock-living) with average flock sizes of the study species is presented in Table 3.1. As prior information on average flock size and its variation was unavailable, data on the birds residing in the study area were collected regularly during censuses together with supplementary observations. These data were critical for density estimation using point counts and line transects. Due to the dense vegetation, not all flocks that were seen could be enumerated completely; data were discarded when there was any ambiguity. Only flocks seen close (< 15 m) to the observer were counted, particularly where visibility was not obstructed by dense vegetation and the flocks could be followed for reconfirmation. This was frequently not possible during regular censuses as attempting to confirm flock size would have required interrupting the census or leaving the transect or count station. Thus, usually fewer than half the flocks seen during the census could be fully counted and supplementary observations were essential. In many cases, flocks were counted unambiguously as the individual members flew from one tree to another or across the trail (or crossed it on the ground, e.g., Puff-throated Babbler). All flock-size data used in this study were collected in the vicinity of the two study plots (see below) during the morning hours (0600 – 1000 h), but supplemented by a few observations from 1600 – 1830 h. The data were collected over the same period as the censuses—during the breeding season and the early southwest monsoon following the breeding season. During the latter period, some flocks included recently-fledged young birds (usually one or two individuals), although this did not change the average flock size substantially. Hence data from all months considered for density estimation were pooled for estimating average flock size and its standard deviation (Table 3.1).

Table 3.1: Study species, habitat-niche, diet, and flock size in the Sengaltheri rainforests, Kalakad-Mundanthurai Tiger Reserve.

S. No.	Species	Habitat-niche	Diet-guild	Flock size		
				Mean	SD	*N*
1.	White-cheeked Barbet *Megalaima viridis*	Canopy	Frugivore	1.23	0.44	13
2.	Asian Fairy Bluebird *Irena puella*	Canopy	Frugivore-nectarivore	1.96	0.66	23
3.	Scarlet Minivet *Pericrocotus flammeus*	Canopy	Insectivore	3.06	1.14	17
4.	Greater Racket-tailed Drongo *Dicrurus paradiseus*	Canopy	Nectarivore-insectivore	2.09	0.80	44
5.	Malabar Whistling Thrush *Myophonus horsfieldii*	Terrestrial	Carnivore	1.11	0.32	18
6.	White-bellied Blue Flycatcher *Cyornis pallipes*	Understorey	Insectivore	1.40	0.55	68
7.	Yellow-browed Bulbul *Iole indica*	Mid-storey	Frugivore-insectivore	2.09	0.70	141
8.	Oriental White-eye *Zosterops palpebrosus*	Canopy	Nectarivore-insectivore	7.88	5.38	25
9.	Puff-throated Babbler *Pellorneum ruficeps*	Terrestrial	Insectivore	1.79	0.72	42
10.	Indian Scimitar Babbler *Pomatorhinus horsfieldii*	Understorey	Insectivore	2.39	1.00	33
11.	Brown-cheeked Fulvetta *Alcippe poioicephala*	Understorey	Insectivore	5.53	3.66	38
12.	Plain Flowerpecker *Dicaeum concolor*	Canopy	Nectarivore	1.25	0.44	24
13.	Crimson-backed Sunbird *Nectarinia minima*	Canopy	Nectarivore-insectivore	2.18	1.70	126

3.4 METHODS

3.4.1 Study plots and sampling

Two plots of 12 ha each, the Kuliratti and Kakachi plots, were established in Sengaltheri along trails (Figure 3.1). The closest distance between the two plots was 500 m, while their centres were over 1 km apart. Each plot consisted of a central transect 600 m long, marked and numbered every 25 m, and 100 m wide strips on either side of this transect. Both plots had a slight altitudinal gradient from one end to the other—about 50 m for the Kuliratti plot and 110 m for the Kakachi plot. While the former was roughly parallel to a perennial stream for about 300 m, the latter was on a hill slope. Within both plots, tropical rainforest was the major habitat and there was little edge habitat.

Data used for this paper came mainly from sampling carried out during and immediately after the breeding season in 1998 (i.e. during the dry season and south-west monsoon). In order to clarify and add to the data for line transect estimates and territory spot-mapping, some data from the north-east monsoon of 1997 were also used for the 12 species that appeared to be territorial throughout the year. For the Crimson-backed Sunbird, only data from the breeding season (January to May 1998),

when they were usually in pairs, were used for all the methods. During the non-breeding season, Crimson-backed Sunbirds joined in flocks of up to 10 individuals and travelled in mixed-species flocks.

All fieldwork and censuses were carried out by a single observer (the author). Line transect and territory spot-mapping data were collected simultaneously on the same day. Point count censuses were carried out on different days or sometimes on the same day before or after a regular line transect census. In total, approximately ten hours were spent on each plot in line transect censuses and spot-mapping, some additional time being spent for the latter to record bird locations. Less time (about 7 hrs) was spent overall in point-count censuses in each plot.

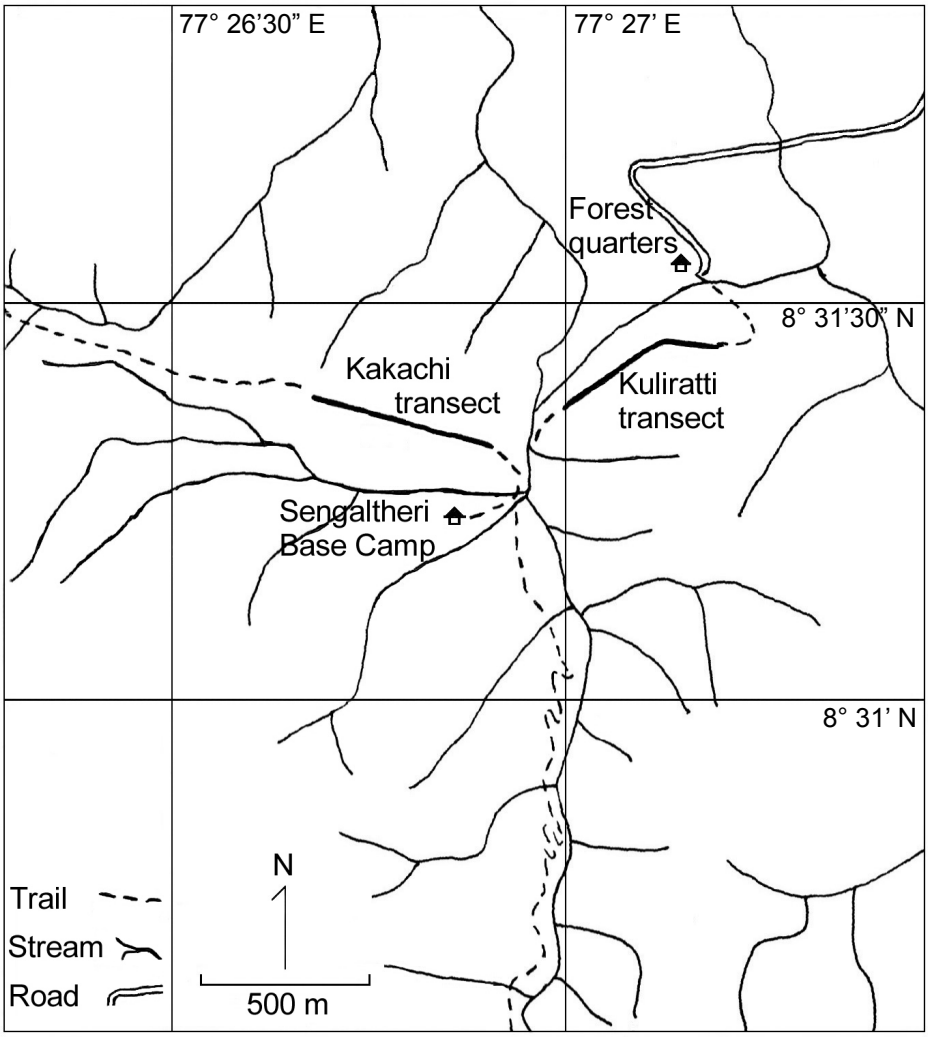

Figure 3.1: Map of the intensive study area, Sengaltheri, in the Kalakad-Mundanthurai Tiger Reserve, showing location of transects.

3.4.2 Line transects

The central transect of each plot was walked for bird censusing twice a month between January and September 1998 (except for May when they were censused once each, January when the Kuliratti transect was censused only once, and April when only the Kuliratti transect was censused once). This entailed repeated coverage of the plot during and after the breeding season (dry season and south-west monsoon). Prior censusing once a month was also carried out on each transect between October and December 1997.

All transects were censused during the first three hours after sunrise when bird activity was highest (Daniels and Hegde 1990). The 600-m-long transect was walked in about one hour, at a slow, uniform pace. All birds seen, heard, or flying under the canopy were recorded as to species, number of individuals (wherever possible), and perpendicular distance in the following metre classes: 0–5, 5–10, 10–15, 15–20, 20–30, 30–50, and 50–100. The distance classes further away were wider to minimise errors in distance estimation (verified using a range finder whenever possible). In total, 980 detections of the 13 species (range 34–196 detections/species) were obtained.

3.4.3 Point counts

Point count censuses were carried out along the central transect of each plot on different days during the breeding season and south-west monsoon. As counts need to be carried out at the time of highest bird activity (Buckland *et al.* 1993), all counts were carried out suring the first three hours after sunrise. That this was the period of highest bird activity was confirmed through point count sampling at hourly intervals between 0600 and 1800 h (Figure 3.2). Activity declines after 0900 h, except for increasing formation of heterospecific flocks that account for greater detection rates between 0900 h and 1100 h (Figure 3.2). Counts were of 5 min duration, starting from the time the observer reached the point. This duration was chosen after preliminary sampling of points for up to 10 min duration. The 10 min count was relatively inefficient (fewer than 1 bird detection per minute after the first 5 min) and resulted in obvious inflation of density due to birds that could be noted entering the plot during the count (Figure 3.3). Careful scanning for birds was also carried out while approaching and leaving the point to spot any undetected birds and these were separately noted. All birds seen, heard, or flying under the canopy were recorded in the following radial distance classes in metres: 0–5, 5–10, 10–15, 15–20, 20–30, 30–40, and 40–50, developing on the recommendations of Buckland *et al.* (1993). Birds estimated to be beyond 50 m were not recorded.

Successive points censused on the same day were always at least 100 m apart to avoid overlap (thus only 6 or 7 points could be censused within each plot on a given day). Since each plot was a relatively small area, points censused on different days overlapped to different extents. Using the trail markers, however, uniform coverage of the plot was ensured over each season. Spacing out points and censusing days made it more likely that bird detections at different points and distance intervals were

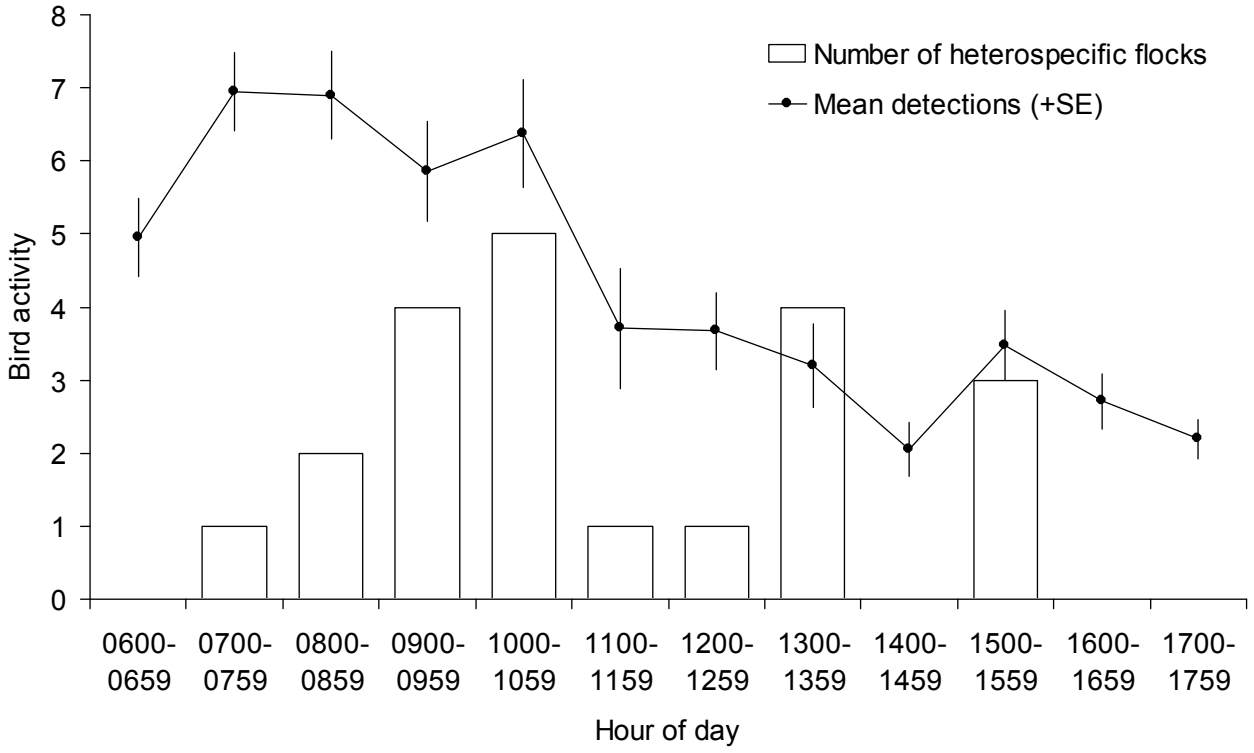

Figure 3.2: Bird activity (overall detections, heterospecific flocks) in relation to time of day in the Sengaltheri rainforest, KMTR. Data from 21 replicate 5-min point counts in each hour-block, collected on clear days during the south-west monsoon of 1998.

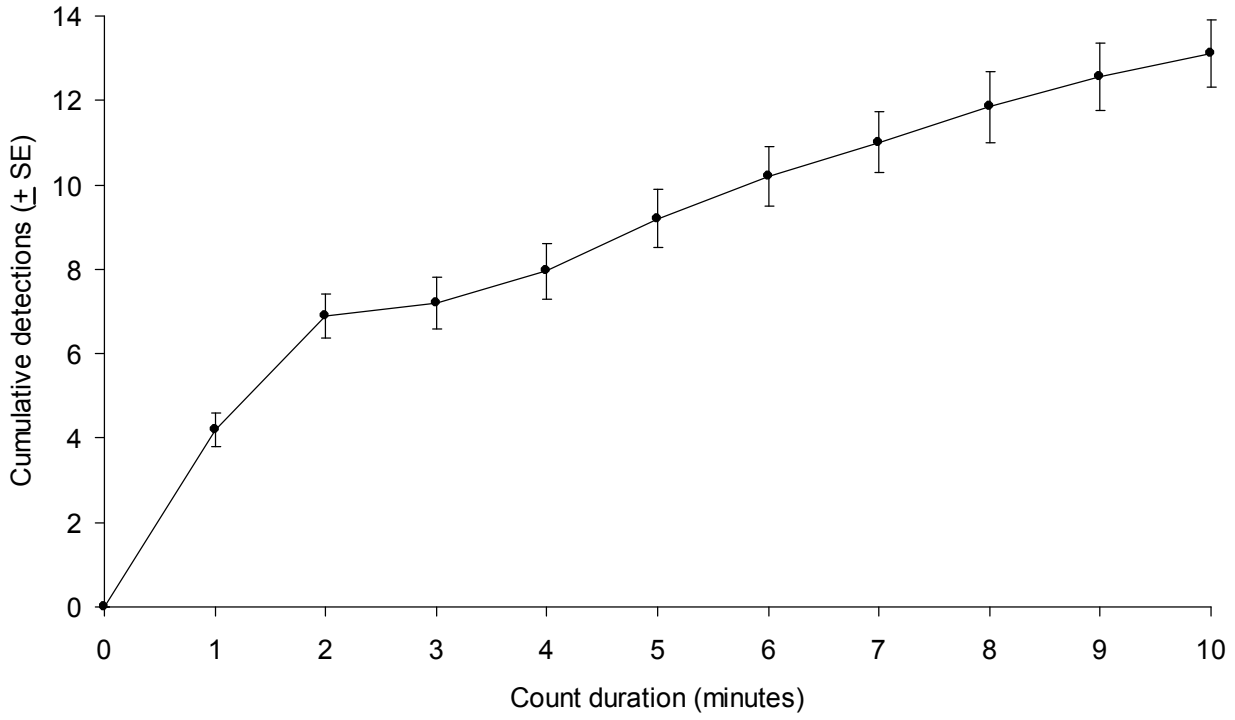

Figure 3.3: Cumulative bird detections in relation to point count census duration in the Sengaltheri rainforests, KMTR. Data from 20 replicate 10-min point count censuses during the early breeding season of 1998.

independent and amenable to standard variable-width point count analyses (Buckland *et al.* 1993). During the dry (breeding) and south-west monsoon seasons, 25 and 35 point count censuses were carried out on each plot, respectively. In total, 532 detections of the 13 species (range 18–98 detections/ species) were obtained.

3.4.4 Territory spot-mapping

Territory spot-mapping as applied elsewhere (Bibby *et al.* 1992, Terborgh *et al.* 1990) was used with minor modifications. With the help of the trail markers positioned at every 25 m along the central transect of each plot, the locations of birds detected during regular transect censuses could be precisely determined. Notes were taken, especially during and after the breeding season, of: (i) location of birds (transect segment, whether left or right, and how far from the line), (ii) detection of singing individuals or pairs, and (iii) occurrence of counter-calling (possibly territorial) between adjacent conspecific individuals, pairs, or flocks. For flocking species, flock territory was estimated. The spot-mapping was restricted to within 100 m on either side of the central transect in order to be directly comparable to the line transects.

The plots were censused seven and eight times each, during the breeding season and south-west monsoon, respectively. Prior coverage (three times each) during the 1997 north-east monsoon helped clarify occurrence and residence status of several species. It was estimated (from the results obtained) that the mapping produced an average of 6.4 detections of each resident pair. It was felt that coverage of the plot was inadequate especially during the breeding season, but more censuses were not possible due to logistics and time limitations. While the data are inadequate for drawing detailed territorial maps in many cases, it seemed adequate to count the number of territorial pairs or flocks in the plot in order to derive a density estimate (see analyses below).

3.4.5 Analyses

Estimates of variable-width line transect and variable-radius point count densities were computed using the program DISTANCE (Version 2.0, Buckland *et al.* 1993, Laake *et al.* 1994). Data from both plots were pooled for analysis. The mean density of clusters (C) was multiplied by average flock size (F) to obtain density of individuals (D). The standard error of the density of individuals (SED) was obtained incorporating SE of density of clusters (SEC) and SE of flock size (SEF) using Goodman's (1960) formula: $(\mathrm{SE}D)^2 = C^2 \cdot (\mathrm{SE}F)^2 + F^2 \cdot (\mathrm{SE}C)^2 - (\mathrm{SE}C)^2 \cdot (\mathrm{SE}F)^2$. Determining SE$D$ over the entire study area would require estimation from randomly placed replicate transects (Buckland *et al.* 1993). It must be noted that in this study the SED is derived from repeated sampling of the same transect as the objective was to estimate densities in the study plots, not to extrapolate to a wider area. All density estimates are reported as number of individuals per 10 ha. Several models of the probability density function (half-normal, uniform, hazard rate, with cosine or polynomial adjustment terms) were

applied to the data for each species. The best model describing the data was chosen on the basis of minimum Akaike information criterion (Buckland *et al.* 1993). For the White-bellied Blue Flycatcher point count data, none of the models gave a good fit due to 'heaping' in the first distance interval, so the first two intervals were combined (0–10 m) for analysis.

For territorial spot-mapping, calling birds and counter-calling individuals were located on a base map. This helped in positioning birds, as well as putative territorial boundaries. Birds detected more than 100 m apart on the same morning census were almost certainly different individuals. Plotting data from successive censuses on the base map revealed distinct clusters of registrations, with counter-calling recorded between the birds of adjacent clusters on several censuses (Figure 3.4). The number of territories that were clearly within the plot was first counted. The number of territories that were only partially within the plot is difficult to determine by this method (Verner 1985). Partial territories were simply counted as 'half' territories in this study. The average number of birds

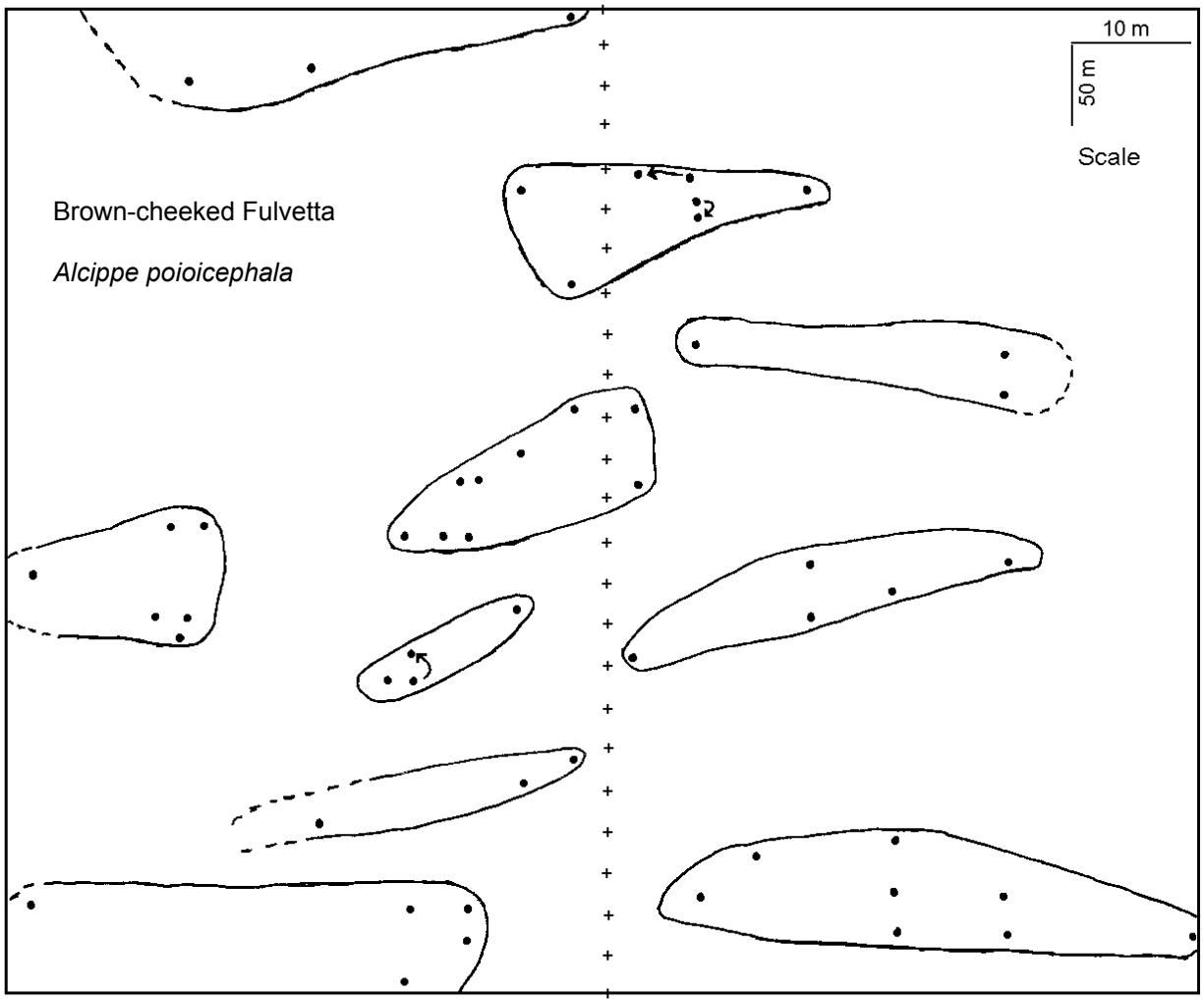

Figure 3.4: An example of a territory spot-map—for the Brown-cheeked Fulvetta along the Kakachi transect. For illustrative purposes, the scale is compressed on the y-axis. Trail markers (+) and bird movements during observation (arrows) are shown.

represented by each territory or cluster was taken as the average flock size rounded off to the nearest integer. For example, eight full and four partial territories represent ten territory equivalents and 20 birds, in a pair-forming species, with average flock size of around two individuals.

The estimated number of birds in both plots was divided by the total area (24 ha) to obtain the spot-mapping density estimate. For the four smallest species (White-bellied Blue Flycatcher, Plain Flowerpecker, Oriental White-eye, and Crimson-backed Sunbird) which had relatively soft calls, no sightings or detections were obtained beyond 50 m. The mapping plot was considered to be only 50 m wide on either side for these species (6 ha in each plot).

Fixed-width strip transect density estimates were calculated using data from within different specified widths on either side of the line: 100 m, 50 m, 30 m, and 15 m. For fixed-radius point counts, radii of 50 m and 30 m were used for density calculations. Density of each species was obtained as follows. The average number of individuals, computed as the product of average number of detections and average flock size, was divided by the area of the strip or circular plot multiplied by the number of replicates.

The following indices of abundance were also calculated:

(i) Line transect flock encounter rate (number of detections of species/km)

(ii) Line transect individual encounter rate (individuals/km, product of average flock size and number of detections of species/km)

(iii) Point count flock detection rate (number of detections of species/point)

(iv) Point count flock detection frequency (percentage of points with detections of species)

(v) Point count individual detection rate (individuals/point, product of average flock size and number of detections of species/point)

(vi) Timed species counts (average number of minutes from start of transect before a species was detected, modified from Pomeroy and Dranzoa 1997, Gibbons *et al.* 1996).

The sequence of analysis was as follows. First, flock sizes, abundance indices, and fixed-width density estimates were calculated. Analysis for density estimation by each method was attempted 'blind' to results of other methods to avoid possible biases in interpretation. First, input files for line transect and point count censuses were created. Before outputs from these were derived using DISTANCE, the territory spot-mapping analysis was completed. The input files were then analysed for outputs of density estimates.

Using STATISTICA computer software, standard Pearson's product-moment correlation and linear regression analyses were used to compare indices and density estimates across methods. Where a number (k) of correlations were being examined, a conservative Bonferroni P-value of $0.05/k$ was used. For comparison of density estimates, regressions through the origin of one estimate on the other were used. The slopes of the regression lines were tested for their departure from unity, which would indicate whether the density estimates differed significantly (Zar 1999).

3.5 RESULTS

3.5.1 Variable-width estimates and spot-mapping

Density estimates for the 13 species are given in Table 3.2. Across methods, it is clear that the two commonest species, Oriental White-eye and Crimson-backed Sunbird, had densities of more than two pairs/ha. Two other species, Brown-cheeked Fulvetta and Yellow-browed Bulbul, had densities of more than one pair/ha. The total density of the 13 species was more than 23 birds/ha.

When the variable-width density estimates from both line transects and point counts were compared with the spot-mapping estimate using linear regression, both showed highly significant positive correlations with the spot-mapping estimates (Table 3.2, Figure 3.5). The regressions were highly significant ($R^2 = 0.99$, $F_{1,12} > 695.6$, $P < 0.001$). The variable-width point count estimates were, however, considerably higher. The slope (1.169) of the regression line of the variable-width line transect density on spot-mapping density differed significantly from unity ($t_{12} = 3.81$, $P = 0.002$). Similarly, the slope (1.955) of the regression line of variable-width point count density on spot-mapping density differed very significantly from unity ($t_{12} = 12.88$, $P < 0.0001$). These two regression slopes also differed significantly from each other ($t_{22} = 9.11$, $P < 0.0001$) indicating a significant difference between methods in the density estimates. The results indicate that on average both

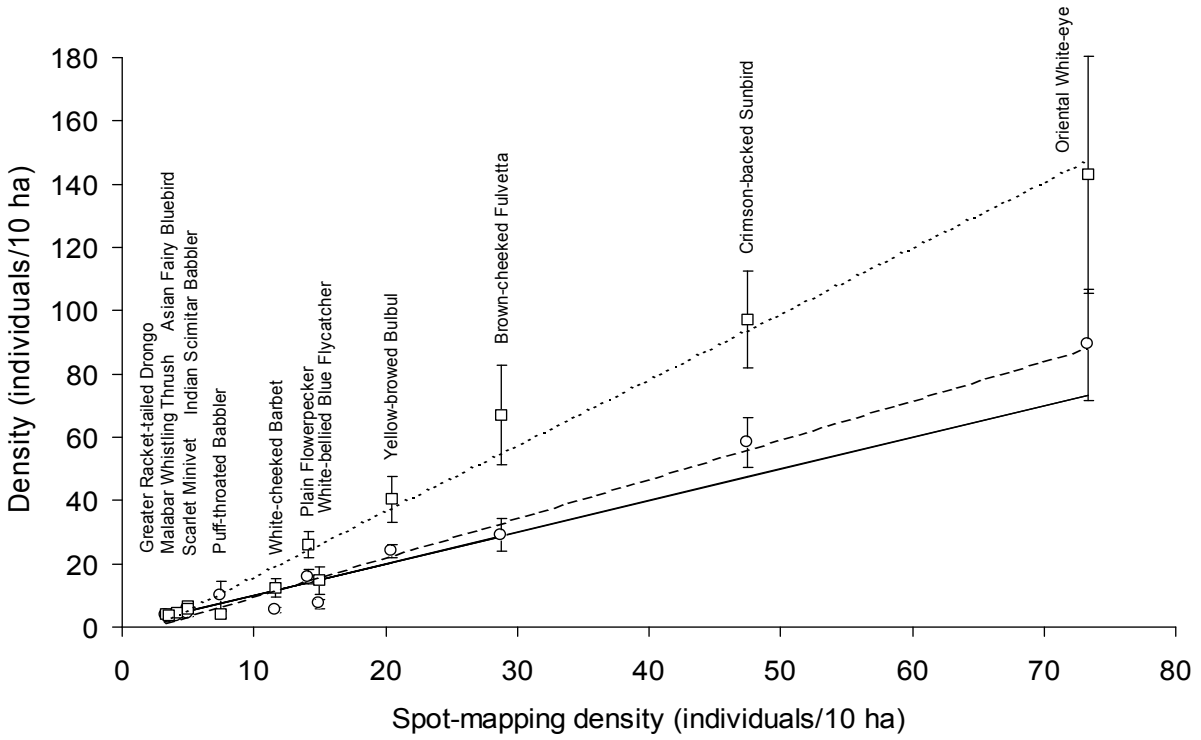

Figure 3.5: Comparisons of variable-width line transect and variable-radius point count densities (means ± SE) with spot-mapping estimates. Dotted and dashed lines indicate estimated regression lines for point count and line transect estimates, respectively, against the spot-mapping densities. The entire line indicates the line of equality (y = x).

methods yield higher density estimates (by 17% for line transects and 96% for point counts) across species than does spot-mapping. In contrast to the regression estimate, the average ratio of estimated line transect density to the spot-mapping density was 0.98 (range 0.45 – 1.31). For point counts, the average ratio was 1.43 (range 0.53 – 2.33). Thus, point counts show greater variation and higher density estimates relative to spot-mapping than do line transects.

To test whether the slopes were strongly affected by the two most abundant species (Oriental White-eye and Crimson-backed Sunbird, see Figure 3.5), the regressions were recalculated without these two species. The slope of the variable-width line transect estimates on spot-mapping estimate (0.965) was then found not to differ significantly from unity (t_{10} = -0.44, P = 0.67). For variable-width point count censuses, however, the slope of the regression line on spot-mapping density remained high (1.856) and significantly more than unity (t_{10} = 4.91, P = 0.0006).

The five species whose point count density estimates were much higher than the spot-mapping estimates, were among the top six most abundant species by spot-mapping (Table 3.2, Figure 3.5). This indicates that point counts produce higher density estimates than spot-mapping for the more common birds. For these five species (Yellow-browed Bulbul, Brown-cheeked Fulvetta, Oriental White-eye, Crimson-backed Sunbird, and Plain Flowerpecker), the proportion of points with more than one detection of the species varied from 0.08 to 0.62. This proportion was unrelated to the magnitude of the difference in density estimates by the two methods, indicating that double counting was not involved. For five species (Asian Fairy Bluebird, Indian Scimitar Babbler, White-bellied Blue

Table 3.2: Density estimates of rainforest birds from variable-width line transects, variable-radius point counts, and territory spot-mapping in Sengaltheri, KMTR. Densities are in birds per 10 ha. Values in parentheses are number of detections and percentage coefficient of variation.

S. No.	Species	Variable-width line transect density	Variable-radius point count density	Spot-mapping density
1.	White-cheeked Barbet	5.28 (83, 17.3)	12.35 (37, 24.2)	11.67
2.	Asian Fairy Bluebird	3.15 (34, 23.3)	4.37 (21, 22.4)	4.17
3.	Scarlet Minivet	5.88 (35, 23.8)	6.49 (20, 24.0)	5.00
4.	Greater Racket-tailed Drongo	3.92 (38, 22.1)	3.99 (18, 24.2)	3.33
5.	Malabar Whistling Thrush	2.86 (76, 17.9)	3.89 (33, 18.7)	3.54
6.	White-bellied Blue Flycatcher	7.30 (43, 17.9)	14.73 (31, 29.0)	15.00
7.	Yellow-browed Bulbul	24.07 (196, 9.1)	40.43 (98, 18.0)	20.42
8.	Oriental White-eye	89.27 (75, 19.7)	143.15 (47, 26.2)	73.33
9.	Puff-throated Babbler	9.81 (47, 47.2)	3.99 (21, 22.6)	7.50
10.	Indian Scimitar Babbler	3.97 (46, 21.3)	5.83 (21, 22.0)	5.00
11.	Brown-cheeked Fulvetta	29.14 (84, 17.2)	67.03 (54, 23.7)	28.75
12.	Plain Flowerpecker	15.82 (108, 14.0)	26.11 (62, 16.1)	14.17
13.	Crimson-backed Sunbird	58.38 (115, 13.5)	97.29 (67, 15.6)	47.50

Flycatcher, Malabar Whistling Thrush, and White-cheeked Barbet), point count densities were closer to the spot mapping values than were the line transect estimates.

3.5.2 Fixed-width and variable-width estimates

Density estimates from fixed-width and variable-width line transects are presented in Table 3.3. The density estimates from strip transects that were 100 m, 50 m, 30 m, and 15 m wide on either side were all correlated positively with the variable-width density estimate (R^2 = 93%, 81%, 97%, and 99%, respectively, $F_{1,12} > 23.7$, $P < 0.001$). The corresponding slopes were 0.21, 0.25, 0.63, and 0.89, respectively. These slopes were all significantly lesser than 1 ($t_{12} < -5.04$, $P < 0.0003$) and indicated density estimates that were lower by 79% (2×100 m strip), 75% (2×50 m strip), 37% (2×30 m strip), and 11% (2×15 m strip) relative to the variable-width line transect estimate.

For fixed-radius point counts, a similar pattern was observed (Table 3.3). Density estimates from both 50-m and 30-m radius counts were positively correlated with variable-width point count density ($R^2 > 0.92$, $F_{1,12} > 165.4$, $P < 0.001$). The slopes of the regression lines for the 50 m (slope = 0.33) and 30 m (slope = 0.65) radii were significantly different from 1 ($t_{12} < -15.74$, $P < 0.0001$). Thus, the 50-m and 30-m fixed-radius counts tended to produce bird density estimates lower by about 67% and 35% across species relative to variable-width point counts; although densities for five species were actually higher in 30-m fixed radius counts (Table 3.3).

3.5.3 Abundance indices and density estimates

Pair-wise correlations between the six abundance indices (Table 3.4) were carried out. Only significant correlations are described here. Three indices that involved only detection of flocks (without including average flock size) were positively correlated with each other—line transect flock encounter rate, point count flock detection rate, and point count flock detection frequency ($r > 0.90$, $df = 11$, Bonferroni $P < 0.05$). The timed species count index was negatively correlated with the above three indices ($r < –0.80$, $df = 11$, Bonferroni $P < 0.05$). The measure derived from timed species counts (average number of minutes before a bird was detected) is expected to vary inversely with the other abundance indices as common birds are expected to be detected sooner.

Similarly, the two measures that involved actual number of individuals (detection/encounter rates of individuals) were highly positively correlated with each other ($r = 0.98$, $df = 11$, Bonferroni $P < 0.05$). Line transect individual encounter rate and point count flock detection rate were also correlated, but the R^2 was low (60%).

Correlations between the different indices and the density estimates were carried out. The four measures that did not involve use of flock size performed poorly and were not significantly correlated with density estimates. In contrast, the line transect individual encounter rate and the point count

Table 3.3: Comparison of fixed width and variable-width density estimates from line transects and point counts for rainforest birds in Sengaltheri, KMTR. Densities are in birds/10 ha.

S. No.	Species	Transects					Point counts		
		2x100 m strip	2x50 m strip	2x30 m strip	2x15 m strip	Variable -width	50 m radius	30 m radius	Variable -radius
1.	White-cheeked Barbet	2.36	3.93	5.03	4.56	5.28	4.83	9.06	12.35
2.	Asian Fairy Bluebird	1.54	2.45	3.18	2.42	3.15	4.37	4.62	4.37
3.	Scarlet Minivet	2.48	4.53	5.90	4.25	5.88	6.49	9.02	6.49
4.	Greater Racket-tailed Drongo	1.84	3.00	4.03	2.90	3.92	3.99	5.55	3.99
5.	Malabar Whistling Thrush	1.95	2.57	2.83	2.40	2.86	3.89	5.23	3.89
6.	White-bellied Blue Flycatcher	1.39	1.39	4.65	7.35	7.30	4.60	9.08	14.73
7.	Yellow-browed Bulbul	9.48	18.29	23.87	24.19	24.07	21.73	33.26	40.43
8.	Oriental White-eye	13.68	13.68	45.00	74.18	89.27	39.30	85.92	143.15
9.	Puff-throated Babbler	1.95	3.23	4.28	6.08	9.81	3.99	5.80	3.99
10.	Indian Scimitar Babbler	2.55	3.43	4.06	3.69	3.97	5.33	4.93	5.83
11.	Brown-cheeked Fulvetta	10.75	19.97	26.03	29.02	29.14	31.68	50.52	67.03
12.	Plain Flowerpecker	3.13	6.19	9.84	14.28	15.82	8.22	17.32	26.11
13.	Crimson-backed Sunbird	14.92	14.92	46.71	57.10	58.38	31.00	66.82	97.29

individual detection rate were both positively correlated with the density estimates from line transects, point counts, and spot-mapping ($r > 0.88$, $df = 11$, Bonferroni $P < 0.05$).

Table 3.4: Indices of abundance of rainforest birds in Sengaltheri, KMTR.

S. No.	Species	LTFER[a]	LTIER[b]	PCFDR[c]	PCFDF[d]	PCIDR[e]	TSC[f]
1.	White-cheeked Barbet	3.8	4.7	0.31	26.7	0.38	54.2
2.	Asian Fairy Bluebird	1.6	3.1	0.18	17.5	0.34	46.5
3.	Scarlet Minivet	1.6	5.0	0.17	16.7	0.51	51.1
4.	Greater Racket-tailed Drongo	1.8	3.7	0.15	14.2	0.31	46.3
5.	Malabar Whistling Thrush	3.5	3.9	0.28	24.2	0.31	30.6
6.	White-bellied Blue Flycatcher	2.0	2.8	0.26	24.2	0.36	45.3
7.	Yellow-browed Bulbul	9.1	19.0	0.82	69.2	1.71	6.7
8.	Oriental White-eye	3.5	27.4	0.39	37.5	3.09	36.9
9.	Puff-throated Babbler	2.2	3.9	0.18	16.7	0.31	34.5
10.	Indian Scimitar Babbler	2.1	5.1	0.18	18.3	0.42	43.0
11.	Brown-cheeked Fulvetta	3.9	21.5	0.45	41.7	2.49	22.0
12.	Plain Flowerpecker	5.0	6.3	0.52	43.3	0.65	21.0
13.	Crimson-backed Sunbird	13.7	29.8	1.12	65.0	2.43	10.2

[a]—Line transect flock encounter rate (average number of flocks/km)
[b]—Line transect individual encounter rate (average number of individuals/km)
[c]—Point count flock detection rate (average number of flocks/point)
[d]—Point count flock detection frequency (percentage of points with detections)
[e]—Point count individual detection rate (average number of individuals/point)
[f]—Timed species count abundance (average number of minutes to first detection)

3.6 DISCUSSION

3.6.1 Population density of rainforest birds

There are no studies from south Asia based on rigorous sampling and analytical techniques that report population densities of rainforest birds. The present study of a mid-elevation, low-diversity rainforest bird community suggests that a few species achieve high densities of over 1 pair/ha (up to 3–4 pairs/ha). In contrast, the most common species occur at densities below 0.4 pairs/ha in the high-diversity Amazonian rainforests (Terborgh *et al.* 1990, Thiollay 1994) or up to a maximum of about 1 breeding pair/ha in a rainforest in Panama (Robinson *et al.* 2000). In 100 ha plots within which around 250 bird species occurred, the total bird density varied from less than 20 birds/ha (Terborgh *et al.* 1990, Thiollay 1994) to 32 birds/ha (Robinson *et al.* 2000). In the more diverse, lower-elevation (350–700 m) rainforests of north-east India, total bird density estimated by using 2×30 m wide strip

transects was 22.7 birds/ha (Raman *et al.* 1998). Reanalysis of this data using variable-width models suggests a density of 25.5 birds/ha (T. R. S. Raman, unpublished data).

Bird diversity in the study area was lower compared to the other areas mentioned above. Bird densities, however, are similar to the values reported for these more species-rich rainforests. This is because the most abundant species achieve high densities, similar to those commonly attained by birds in species-poor temperate forests (Terborgh *et al.* 1990). Bird communities in the rainforests of the Western Ghats, which are relatively depauperate probably due to historical isolation (Daniels *et al.* 1992), thus appear to show possible density compensation effects as noted in other tropical forests (Cody 1983).

3.6.2 Utility of territory spot-mapping

Censusing birds in tropical rainforest poses many challenges due to the high species richness, wide variation in detectability, diversity of social systems from solitary to flock-living, and singing and territory defence by males and females (Terborgh *et al.* 1990). The present study suggests that techniques such as line transects, point counts, and territory mapping, are potentially useful for density estimation and inter-specific comparisons in the Western Ghats, although they do not always give equivalent results. As pointed out by Verner (1985), the choice of technique and its application depends largely on the specific objectives of the study.

The territory spot-mapping method has been regarded widely in the temperate region as being the most accurate for use during the breeding season for territorial birds (Verner 1985). Ornithologists have begun using this technique in tropical forests relatively recently (see Terborgh *et al.* 1990 for a recent application and review of past studies, Thiollay 1994, Robinson *et al.* 2000). The present study indicates that the method can be applied usefully to study territorial rainforest birds in the Western Ghats.

A few caveats, however, need to be added about the use of spot-mapping in this study. First, territoriality needs to be confirmed through use of marked individuals (through mist-netting and colour ringing). This was not possible during the present study, as requisite permits were not available. Thus, this study is only a preliminary attempt at documenting territoriality. Second, the shape and size of the plot chosen for this study were dictated by logistics and were not ideal for mapping. A larger plot is required for mapping some of the larger, wide-ranging birds (e.g., laughingthrushes, treepies, hornbills, and woodpeckers). In addition, making the plot square-shaped rather than rectangular would probably decrease the number of edge territories and increase the accuracy of density estimation. A third factor is the lack of information on seasonal changes in territoriality, flocking behaviour, and social organisation. Future research to fill these lacunae will be valuable to study and monitor bird populations throughout the Western Ghats rainforests, and should be encouraged by the government authorities.

Where time and resources are available, territory spot-mapping should be the method of choice for ornithologists. Besides information on density, territory sizes, and social organisation and behaviour, mapping can yield insights into area requirements of rainforest birds and spatial patterns of plot occupancy or diversity (Terborgh *et al.* 1990), intra- and inter-specific territoriality (Robinson and Terborgh 1995), and bird distribution in relation to resources or habitat. For instance, mapping yielded clear clustering of bird territories in relation to food or habitat for species such as Plain Flowerpeckers (more territories in an area with greater infestation of parasitic mistletoes on trees), and Malabar Whistling Thrush (along streams and ravines), while other species showed a more uniform distribution (e.g., Yellow-browed Bulbul, Brown-cheeked Fulvetta, Oriental White-eye). The major drawback of spot-mapping is the greater time and effort needed; for a given effort it may be possible to survey fewer areas with mapping than with other methods such as transects. Where the goal is coverage of more areas or studying large-scale species-habitat relationships, transects or point counts may prove more useful (Ralph *et al.* 1993, 1995).

3.6.3 Comparison of census methods

When compared with density estimates from spot-mapping, variable-width line transects gave more accurate estimates than the point count method, particularly for the common bird species. The line transect method was also found convenient for field use as the majority of bird detections were close to the line, making distance estimation and counting easier. The estimation of higher (by about 17%) densities across species may be due to: (i) some consistent bias in underestimating distances, (ii) presence of non-territorial 'floaters' and non-breeding young that are not counted in territory mapping, and/or (iii) the influence of the two most abundant species (because the regression slope was close to unity when they were excluded). Since the accuracy of distance estimation was checked regularly using a range finder, and in relation to marked trees in the plots (especially in the critically important first two distance bands), the first reason appears unlikely. The second factor appears plausible and may have worked in combination with the third to produce the slightly higher density estimates.

Across species, variable-radius point count censuses gave density estimates that are nearly twice that obtained by spot-mapping. Past research has also suggested that line transects produce more accurate density estimates than point counts (Järvinen 1978, Verner 1985). Point counts have been reported to produce both higher (Verner and Ritter 1985) and lower (DeSante 1981, 1986) estimates of density in relation to transects or mapping in comparative studies. Verner (1985) has pointed out that because the area sampled with point counts increases geometrically with distance from the observer, but only linearly with transects, violation of assumptions produces much larger errors in density estimation. Although detectability declines with distance, area increases geometrically, and so most bird detections are at some distance away from the observer (typically 20–30 m in this study) making accurate distance estimation more difficult.

In the present study, point counts performed well for three species of relatively cryptic, sedentary, understorey birds, and two canopy birds that are most often detected by calls. The method performed most poorly for the most abundant species, which tended to be vocal and mobile. The higher point count density estimates for these species were, however, not due to double counting. Instead, the problem may be caused by mobility. Mobility of birds may seriously bias density estimates, especially those from counts of longer duration (Scott and Ramsey 1981). In point counts, as the observer remains stationary for 5 min, during which time birds may enter the plot, the estimated density would tend to increase cumulatively with time spent counting (the number of detections did increase cumulatively up to at least 10 min in preliminary trials during this study).

3.6.4 Fixed-width estimates

Fixed-width transects and point counts assume a complete count of all birds within the specified strip or radius. This is very unlikely in most habitats, particularly in the dense and structurally complex moist forests. Factors such as visibility, cryptic appearance of birds (Verner 1985, Terborgh *et al.* 1990), and sound attenuation effects (Waide and Narins 1988) imply that a number of birds will be missed. Many species are not detected at all beyond 30 or 50 m. As expected from line transect theory (Burnham *et al.* 1985, Buckland *et al.* 1993), wider strips produced lower density estimates than variable-width estimates. Even density estimates from strips as narrow as 15 m tended to be lower than variable-width estimates, although for a few species, the densities estimated with these very narrow strips were almost identical by the two methods. Thus the use of wide strips of 50 m (Pramod *et al.* 1997) or 100 m (Daniels *et al.* 1992) is likely to give lower density estimates. It may also give inaccurate estimates of relative abundance because the proportion of individuals detected differs widely across species (Verner 1985). Although relative bias declines with strip transect width, density estimates from very narrow or very wide strips tend to suffer from wider variance (Burnham *et al.* 1985). A strip width of 30 m on either side may be a useful compromise where application of variable-width line transects is difficult.

Similar considerations apply for fixed-radius point counts. However, although smaller radii reduce bias in fixed-radius point counts, the loss of precision may be even greater than for fixed-width line transects. This is because the radial nature of sampling implies a substantial fraction of detections (sample size) comes from birds over 20 or 30 m away from the observer and one cannot afford to exclude these from the analysis. Very small areas are sampled with radii of <20 m and these may have too few detections. As densities from even 50 m radii were highly positively correlated to variable-radius point count, line transect, and spot-mapping densities, these may be used for general comparisons and for determining relative abundance of birds. That relatively higher estimates may be obtained for some common, vocal, and mobile species needs to be kept in mind.

3.6.5 Conservation monitoring of bird populations

Accurate estimates of bird density are essential for many studies including diversity-abundance relationships, biomass, and ecological productivity (Wiens 1989, Terborgh *et al.* 1990, Thiollay 1994). For many community studies and basic monitoring of bird population trends, however, abundance indices may suffice (Verner 1985, Wiens 1989). Valid methods for inter-specific comparisons are also essential to understand the underlying causes of changes seen in the relative abundances of species along natural or disturbance gradients (Furness and Greenwood 1993). For large-scale monitoring programmes involving amateur and professional ornithologists, the choice of relatively simple field techniques is an added asset (Terborgh 1989, Bibby *et al.* 1992).

Fixed-width methods may be more easily applicable in monitoring programmes, because it is easier to record whether birds are within one fixed distance than it is to record perpendicular or radial distances to all detections. Analysis of fixed-width data is also relatively straightforward. Strip transects of 30-m width may be recommended for general use where terrain conditions permit. In difficult terrain, where straight trails or transects are impossible, fixed radius point counts of 30- or 50-m width may be used. Point counts, in particular, are widely used in other regions for population monitoring (Ralph *et al.* 1993, 1995) and may prove particularly useful for the census of cryptic, sedentary rainforest birds. Furthermore, in the same time that it takes to census one line transect, observers could sample many replicate point counts (usually 8-9, in this study), which can be more useful for statistical analyses. Spot-mapping may be useful for monitoring populations of territorial birds in relatively small plots, or where monitoring is targeted at one or a few species, but is too time- and energy-intensive for large-scale use.

Among the indices, timed species counts performed poorly and are discouraged for general use. This index also showed very high variability for most species (CV of c. 100%). Spurious values of the index may be obtained where plots or transects are repeatedly sampled because some territorial birds are seen at the same place or time on each census, irrespective of their abundance. At the least, monitoring efforts using indices should attempt to obtain encounter/detection rates of individuals in replicate transects or point counts. For this, distance traversed/number of points covered and flock size must be known for individual species.

For monitoring programmes, careful attention must be paid to standardise and specify widths, amount of time spent in censuses, and effort in distance or number of points covered (Ralph et al. 1993). Observers participating in monitoring programmes also need to be trained in on-site distance estimation, identification of birds by sight and call, and careful collection of flock size data. Further research involving the application of more than one method at specific localities over several years will help to identify what indices are suitable to monitor particular species over time (Ralph *et al.* 1993).

3.7 SUMMARY

Studies comparing different bird census methods are useful for assessing relative biases, synthesising data across studies, and designing bird population monitoring programmes. This study in mid-elevation tropical rainforests in the Western Ghats compared bird density estimates from line transect, point count, and territory spot-mapping methods and various abundance indices. Inter-specific comparisons were made using data for 13 common resident bird species, including two endemics. Bird densities were similar to those in other tropical rainforest regions that are more species-rich, indicating possible density compensation effects. The two most abundant species attained densities of over 2 pairs/ha, unlike other lowland tropical rainforests and more like temperate forests. Variable-width line transect density estimates were highly correlated with, but slightly (17%) higher than, those produced by territory spot-mapping. Although densities from variable-width point counts and spot-mapping were highly positively correlated, the estimates were 95% higher on average in the former. Higher density estimates relative to spot-mapping were produced mainly for the most abundant species probably due to their mobility and the inclusion of additional individuals that enter the count area during the count period. Fixed-width strip transects and point counts produced density estimates that were highly correlated with but significantly lower than variable-width estimates. Indices involving detection/encounter rate of individuals were significantly correlated to density estimates, while timed species counts and detection/encounter rate of flocks were not. This was because variation in flock size across species is incorporated only in the former measures. Wherever possible, territory spot-mapping and line transects are recommended for density estimates; the former may yield additional information on spatial distribution of birds. Fixed-width transects or point counts, being easier to apply, may be used for large-scale monitoring programmes; point counts may be particularly useful in difficult terrain or for cryptic species. Inter-specific variation in flocking systems and the poor visibility in dense rainforest vegetation indicates the need for care in collection of data on flock size and its variation, which are necessary for estimating the density of individuals. The variation across methods suggests the need for further research using multiple methods across years and marked individuals to verify territoriality and accuracy.

CHAPTER 4

Bird community structure along an elevational gradient in a tropical rainforest

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CHAPTER 4

Bird community structure along an elevational gradient in a tropical rainforest

4.1 INTRODUCTION

Understanding the patterns of distribution of tropical rainforest birds along elevational gradients is as crucial for ecologists trying to unearth underlying principles of community organization as for conservation biologists striving to conserve these species in montane regions. Nevertheless, there have been relatively few well-documented studies of elevational distributional patterns of tropical rainforest birds. The pioneering work of Terborgh (1971, 1977) describing the multifaceted nature of elevational patterns still stands tall among these studies. In the highly diverse bird communities of the Cordillera Vilcabamba in Peru, the studies of Terborgh (1971, 1977, 1985a) and Terborgh and Weske (1975) indicated that competition played a defining role in the elevational distributions of two-thirds of the bird species, while gradients and ecotones influenced equal parts of the remaining one-third.

Since Terborgh's path-breaking work, research on elevational distributional patterns of birds has tended to focus on three major aspects—variation with elevation in richness (or diversity), range sizes, and turnover rates of bird species—and on one region with relatively well-documented information on bird elevational distributions, the Neotropics (Rahbek 1997, Patterson *et al*. 1998, Stotz 1998, Blake and Loiselle 2000). A pattern of decreasing species richness with increasing elevation is believed to mirror the well-recognised latitudinal gradient in species richness (MacArthur 1972, Stevens 1992) and has been considered general enough to merit its inclusion in standard texts

dealing with the subject (Begon *et al*. 1990, Whitmore 1998). Although several studies on taxa ranging from invertebrates to mammals have corroborated the pattern of monotonic decline in species richness with elevation (Lawton *et al*. 1987, Graham 1990, Patterson *et al*. 1996, 1998), many have refuted this pattern (Janzen 1973, Olson 1994, Rahbek 1997, Stotz 1998, Blake and Loiselle 2000).

In contrast to the 'general' gradient pattern, species richness may show a non-monotonic, hump-shaped pattern with diversity peaking at mid-elevations. This pattern may manifest itself when data are corrected for sampling effort for local species richness (Terborgh 1977, Patterson *et al*. 1996) or area for regional species richness (Rahbek 1997). This pattern parallels changes seen on diversity-productivity gradients (Rosenzweig and Abramsky 1993, Rosenzweig 1995). Such models need to be evaluated against patterns expected from null models that assess the effects on species richness of geometric constraints in the elevational ranges of species. Colwell and Hurtt (1994) examined null models that placed species ranges randomly along the elevational gradient between two hard boundaries (upper and lower) beyond which species cannot extend. The models predict an inverse U-shaped pattern of species richness with peaks (or plateaus, depending on the constraints) occurring at mid-elevations (Colwell and Hurtt 1994, Rahbek 1997, Veech 2000). This pattern, labelled the 'mid-domain effect' (Colwell and Hurtt 1994, Colwell and Lees 2000), has conceptual antecedents in the 'two-hit broken stick' model of MacArthur (1957), extended by others (Pielou 1975, Dale 1986, 1988).

The variation in distributional range sizes of constituent species may itself be influenced by macroecological factors such as habitat availability, environmental tolerance, dispersal ability, and abundance (Brown 1995, Gaston 1996). Elevational range sizes of species may increase with increasing elevation, as suggested by Stevens (1989, 1992) in an extension of Rapoport's rule (Rapoport 1982) to elevational gradients. As higher elevations experience wider climatic fluctuations, species found at higher elevations are expected to tolerate a wider range of environmental conditions and hence have wider elevational ranges. Lower elevations that contain species of more restricted distribution, in addition to wide-ranging species from higher elevations, thus have more species, resulting in monotonic decline in species richness with increasing elevation (Stevens 1989, 1992). Rapoport's rule has recently been the subject of intense debate (Gaston 1999, Gaston *et al*. 1998, Taylor and Gaines 1999, Chown and Gaston 2000 and references therein).

All species cannot be treated as equivalent in their distribution ecology and one therefore needs to examine factors influencing turnover of species along the altitudinal gradient. Turnover rates (faunal congruity of Terborgh 1971) may increase with elevation (Rahbek 1997) or show peaks and troughs corresponding to transition zones between lowland and montane avifaunas (Patterson *et al*. 1996, Stotz 1998). Patterns of species richness may also vary in relation to avian diet guild and habitat structure (Terborgh 1977, Blake and Loiselle 2000) or between typically lowland *versus* montane species (Stotz 1998). Changes in habitat structure and tree species composition are known to influence bird community structure along successional gradients, wherein sites that are more similar structurally

and floristically tend to have more similar bird communities (Raman *et al*. 1998). Along elevational gradients, however, the relative importance of differences between sites in habitat attributes in contrast to elevation *per se*, has been poorly documented.

The present study explores variation in bird community and guild structure, and species abundances, range sizes, and turnover rates along an elevational gradient in a tropical rainforest of the Western Ghats of India. This region, although recognised as a global biodiversity hotspot (Olson and Dinerstein 1998, Myers *et al*. 2000) and an endemic bird area (Stattersfield *et al*. 1998), is peculiar in being relatively depauperate in its rainforest bird community due to historical isolation from larger tracts of rainforest in northeast India and southeast Asia (Daniels *et al*. 1992). Here, I explore the following questions. How do bird community attributes vary with elevation in this tropical rainforest bird community? Does species richness show a monotonic decline with elevation or a hump-shaped pattern due to the 'mid-domain effect'? Are elevational trends consistent across different diet-guilds? Do the elevational range sizes of species vary in relation to their abundance as predicted by macroecological theory or according to elevation as determined by Rapoport's rule? How well are patterns of species richness predicted by simple null models? Finally, what factors influence turnover in species composition with elevation? Does elevational distance and degree of change in habitat influence and correlate with change in bird community composition or are turnover rates estimated accurately by null models that simulate non-equilibrium dynamics?

4.2 STUDY SITES

This study was carried out in Kalakad-Mundanthurai Tiger Reserve, the details of which are given in Chapter 2. The intensive sites chosen for bird community sampling were located around forest camps at Kannikatti (740 m asl, 8°37' N and 77°16' E), Sengaltheri (1040 m asl, 8°31' N and 77°26' E), and Kakachi (1220 m asl, 8°33' N and 77°24' E) in KMTR. These areas contain rainforests ranging in altitude between 500 m and 1,400 m, which are contiguous with rainforests elsewhere in the Reserve. The terrain is rugged, mountainous, and drained by many perennial streams and two major rivers, Manimuthar and Tambiraparani.

Fourteen sites located along an elevational gradient of 500 to 1,400 m were selected around the three base camps (four accessed from Kannikatti, six from Sengaltheri, and four from Kakachi). Although I attempted to select the sites randomly, site selection was constrained by the need to obtain representation of different elevation zones as well as by logistics and accessibility. As all fieldwork had to be carried out on foot, these sites were located within a 6-km radius of the base camps and were reached along existing forest and animal trails. All sites were in relatively undisturbed rainforest over 5 km away from human settlements, except an old (> 20 year) selectively-logged forest site near Kodayar settlement, a low-elevation undisturbed site near the Injikuli tribal settlement, and a site in Sengaltheri that had a low level of fuelwood and timber extraction from cardamom estate workers

(prior to being abandoned in 1995). The locations of each sampling site were marked on Survey of India maps (1:25,000 scale) using natural topographic landmarks, cross-verified with readings from a hand-held global positioning system receiver (GPS).

4.3 METHODS

4.3.1 Bird surveys

The emphasis was on sampling all sites for birds in a relatively uniform and efficient manner during the main breeding season. The fixed-radius point count method was used to survey bird populations in each site. This method has been widely applied to survey birds, and is especially useful in dense vegetation and difficult terrain as in the study area (Karr 1981, Verner 1985, Hutto *et al*. 1986, Bibby *et al*. 1992, Ralph *et al*. 1995, Gibbons *et al*. 1996). Point count surveys were carried out during the first three hours after sunrise when bird activity was highest. Count duration of 5 min, starting from when the observer reached the point was found suitable (Chapter 3). Points were carefully scanned for birds while entering and leaving the plot to record individuals that may have otherwise been missed. All birds seen, heard, or flying under the canopy were recorded in the following radial distance classes (in m): 0–5, 5–10, 10–15, 15–20, 20–30, 30–40, and 40–50. I used densities estimated by the fixed radius approach as they were highly correlated to variable-radius point count estimates across species (Buckland *et al*. 1993, Chapter 3). Since all sites were in relatively undisturbed and structurally similar rainforest vegetation (see Results) biases due to detectability differences between sites were unlikely to have been pronounced or correlated with altitude to affect the patterns.

Each sampled site represented an area of around 12-15 ha lying at the designated altitude and was surrounded by was contiguous rainforests on at least three sides. Within each site a 600 – 700-m long transect or narrow animal trail was marked at 25 m intervals for the point count surveys. In each site, 25 point count surveys (yielding 167–247 detections and an estimated 334–597 individual birds per site) were carried out, excluding the Kodeyar site where only 18 point counts were sampled because of logistical difficulties. The trail markers were used to locate points. I attempted to ensure independence of data points to the extent possible by spacing out points and survey days. Successive points sampled on a given day were at least 100 m apart to avoid overlap and intermediate points in each site were sampled on different days. Although points sampled on different days overlapped to some extent, the procedure followed ensured uniform coverage of the site. Sampling of all sites around Sengaltheri and Kakachi was carried out mostly between February and May 1998, over the peak breeding season when resident and migrant birds were present in the plots. For reasons of logistics, the four sites around Kannikatti were sampled only in March 1999. Resident birds are considered separately in the analyses reported in this chapter.

4.3.2 Vegetation sampling

In each of the 14 sites, densities of trees greater than 30 cm girth at breast height (GBH at 1.3 m) were estimated using the point-centred quarter method (PCQ, Krebs 1989). Thirteen PCQ plots, with successive plots spaced 50 m apart, were measured in each site, giving a sample of 52 trees per site. Comparison with two completely enumerated (> 1,800 stems) 1 ha plots in Sengaltheri (T3) showed that the density estimates from this PCQ sample was <2% different from the more laborious enumeration, hence the PCQ method was adhered to. All trees in the PCQ plots were identified to species, or in a few cases to genus, using available field guides (Gamble 1935, Pascal and Ramesh 1997). Using a tape measure, distance from plot centre to the middle of the bole and GBH were recorded for each tree. At each of the 13 PCQ plots, 2 m radius plots were laid to enumerate shrubs. In addition, the number of cane plants and the presence or absence of bamboo within 5 m radius was recorded.

Canopy and leaf litter variables were measured at 25 points, evenly spaced 25 m apart, in each site. Elevation readings were also taken at these points using an altimeter. Canopy height was measured using a rangefinder. Percentage canopy cover was measured using a spherical densiometer at each of the 25 points in each site. Vertical stratification was assessed at these 25 points following Raman *et al*. (1998). The presence or absence of foliage was noted in the following height intervals (in metres): 0–1, 1–2, 2–4, 4–8, 8–16, 16–24, 24–32, and > 32, directly above and in a 0.5 m radius around each point. Leaf litter depth on the forest floor was measured using a calibrated wooden probe at each point. As ground vegetation and litter were disturbed along trails, the samples were taken 10 m away from trails into the rainforest interior.

4.3.3 Analyses

4.3.3.1 *Bird community parameters*

The cumulative list of bird species recorded in each site was used as a basic measure of bird species richness. However, because only 18 point counts were sampled in one site, I obtained standardised estimates of bird community parameters for all sites for 17 sampled points. Using the program EstimateS (Colwell 1997), I performed 100 Monte-Carlo simulations selecting 17 samples at a time (without duplicating samples) to estimate the following parameters and their standard deviations (see Colwell and Coddington 1994 for a discussion of the utility of this approach).

1. Bird species richness, measured as the cumulative number of species;
2. Bird abundance, estimated as the number of individual birds/ha;
3. Shannon-Weiner diversity, calculated as $-\Sigma\, p_i \ln p_i$, where p_i is the proportion of the i^{th} species and the summation is across all species in the pooled samples;

4. Rarefaction richness, standardising for sampling effort using Coleman rarefaction curves (Coleman *et al*. 1982, Colwell 1997);
5. Bootstrap species richness, an incidence-based estimator denoted as

   $S_{boot} = S_{obs} + \Sigma (1 - p_k)^m$

   where p_k is the proportion of m samples with species k and the summation is across all S_{obs} species in the pooled samples; and
6. Chao 1 richness, an abundance-based estimator of species richness (see Colwell 1997 for the formula and correct variance estimator of this index).

Unlike bird species richness and rarefaction richness, the bootstrap and Chao 1 richness indices estimate richness, including 'missed' species, using a form of extrapolation depending on species incidence (bootstrap) or abundance (frequency of singletons and doubletons, Colwell 1997).

The input for the analysis for each site was a matrix of abundances of individual species across the replicate point count samples. In each sample, many bird detections were made by calls and the number of individual birds could not be counted in the field. For each species, however, information on flock sizes (a flock representing one to many individuals for this purpose) was collected during surveys and opportunistic observations. For species with fewer than 10 aural detections, the number of birds comprising a given detection was assumed to be the average flock size of the species rounded to the nearest integer. For more frequently detected species, a flock size was randomly assigned to each detection through a Monte-Carlo procedure from the sampling distribution of flock sizes for that species. This allowed estimating the number of individual birds of each species in the point count surveys.

In addition to the above parameters that describe the bird community at each site, I obtained smaller scale point richness and abundance estimates averaging across replicate point count surveys in each site. The average number of species, detections, and individuals per point and their standard errors were estimated for all species combined and for resident species alone.

Cumulative species richness and abundance (individuals/ha) of birds belonging to eight diet-guilds were also estimated using the point count survey data. Birds were classified as bark-surface feeders, carnivores, frugivores, nectarivore-insectivores, omnivores, and canopy, understorey, and terrestrial insectivores, following natural history information in Ali and Ripley (1983) and direct observations.

4.3.3.2 *Vegetation*

For each site, tree density and basal area were calculated using the PCQ method (Krebs 1989). Average values across replicate sampling points in each site were calculated for other vegetation and site variables: shrub, cane, and cardamom densities, leaf litter depth, canopy height, cover, and rank, and altitude. Vertical stratification was measured as the average number of strata with foliage across

the 25 points sampled in each site. The coefficient of variation of this index reflected variation in foliage distribution across points and was used as an index of horizontal heterogeneity (following Raman *et al*. 1998). The total number of tree species recorded in the PCQ plots was recorded as a measure of tree species richness. Relationships between bird community and vegetation variables were assessed using Kendall correlations (Siegel and Castellan 1988).

4.3.3.3 *Elevational range sizes*

Elevational range size of each species was estimated as the difference between the maximum and minimum altitude at which the species was recorded in the point count surveys. For a few species that were absent in some intervening sites, these 'holes' were ignored in estimating the elevational range and their absence in the point count surveys was attributed to chance effects of sampling. In most cases, this assumption appeared valid, as the species was recorded (usually occurring at low density) in supplementary observations made at or near the site during the study. The midpoint of each species range was taken as the average of the upper and lower limits. In addition, a weighted midpoint was estimated using the abundance of each species in each site.

4.3.3.4 *Species turnover*

Similarity in bird community and tree species composition between sites was computed using the Morisita index that is least sensitive to sample size effects (Wolda 1981). An index of similarity in foliage profile was also computed using the Morisita index using the data on number of points with foliage in different vertical strata (following Raman *et al*. 1998). The matrix of pairwise dissimilarities (100-Morisita index in %) in bird community composition was related to corresponding matrices of similarity/distance in tree species composition, foliage profile, elevation, and geographic distance between sites using Mantel tests (Manly 1994). Geographic distance between sites was measured as the straight-line distance between sampling sites marked on the Survey of India maps (1:25,000 scale). Statistical significance of Mantel tests was assessed through 10,000 random permutations. To examine the independent effects of different variables partial Mantel tests, derived from the Kendall tau approach, were used (Hemelrijk 1990). The tree and bird community similarity matrices were also used to ordinate study sites using multidimensional scaling (Manly 1994).

4.3.3.5 *Statistical analyses and null models*

I used correlation and regression techniques to assess statistical significance of elevational trends. Linear and non-linear (chiefly quadratic) regressions were applied to describe spatial trend data. I also used non-parametric Kendall (*tau*) rank-order correlation coefficients to assess statistical significance (Siegel and Castellan 1988).

To address the problem that estimates of species richness along a spatial gradient may be non-independent and to assess the mid-domain effect (Colwell and Hurtt 1994, Colwell and Lees 2000), I used the null model of Veech (2000). This null model has been found to have high statistical power for curves consisting of at least 10 richness estimates from a total pool of 20 or more species (Veech 2000). This model randomly places the elevational range of each species along the gradient with the constraint that range widths are kept fixed as observed. The elevational gradient between 500 and 1400 m was divided into 18 zones of 50 m width. I used 1000 simulations to first obtain an expected species richness curve (the average random curve) along this gradient. Using data on elevational range of each species, the observed species richness of each zone was calculated. This was compared to the average random curve to obtain a mean displacement, D, where $D = (\sum d_j)/18$, where d_j is the absolute difference in species richness between the two curves being compared for each of the 18 zones (Veech 2000). A further 1000 simulations of the data were used to determine the distribution of D values in each run and to assess statistical significance.

I also used null models to assess the likelihood of obtaining, under the null model assumptions, estimates equivalent to two measures of the average similarity between sites in bird community composition. These measures were: (i) average similarity between all possible pairs of sites ($N = 91$ comparisons), and (ii) average similarity between successive sites along the elevational gradient ($N = 13$ comparisons). The Jaccard index (Magurran 1988, Krebs 1989) was used to measure similarity in bird community composition. Five null models were evaluated.

i) Unconstrained model: there were no constraints on the species richness or range width in this model except that the total number of occurrences in the species by sites matrix was kept constant.

ii) Saturation model: the number of species in each site was kept constant (fixed column totals);

iii) Distribution model: the number of sites each species occurred in was kept constant (fixed row totals);

iv) Doubly constrained model: the number of species per site and the number of sites occupied by a species were both kept constant (fixed row and column sums) by a procedure equivalent to the Knight's tour algorithm (Sanderson 2000).

v) Range-contiguity model: this model simulated, in addition to the distribution constraint, the contiguity of ranges of species along the gradient. Simulations showed that species occurrences were distributed more contiguously along the gradient than expected by random placement ($P < 0.001$). Using the observed occurrences in the species-by-site matrix, the relative probability of occurrence in any one of the 12 intermediate sites (excluding the 2 'edge' sites—the lowest and highest site) was found to be enhanced by a factor of 9.0 if the species also occurred in sites immediately above and below and by a factor of 4.5 if it occurred only in one adjacent site either above or below. These

enhancement factors were in relation to the probability of occurrence in a site when the species was absent from both adjacent sites on the gradient. For the edge sites, occurrence was enhanced by a factor of 3.6 if the species occurred in the adjacent site in relation to occurrence when it was absent in the adjacent site. These were then used to distribute occurrences in simulations to produce probabilistic contiguous distributions.

For each model I carried out 5000 simulations (randomised matrices) in each of which the average similarity between all possible pairs of sites and the average similarity between successive sites along the gradient was calculated using the Jaccard index (Morisita index was not used as models with abundance are too elaborate). The distribution of values so obtained was compared to the observed average similarity values in order to assess which of these non-equilibrium models could most accurately estimate the observed pattern of species composition and turnover in the study area.

As pointed out by a number of workers (Diamond and Gilpin 1982, Farnsworth and Ellison 1996, Stone *et al*. 1996, Sanderson 2000), these models attempt to simulate chance effects and different biological constraints on the assembly of species communities. The models reflect a hierarchy of complexity from least constrained to more circumscribed, and the quest is for the most parsimonious model that can predict the real-world pattern. The unconstrained model simulates a situation reflecting historical factors influencing the distribution of species, such that the occurrence of a certain number of species across a set of sites is largely driven by chance and at any given time the species by site occurrence matrix would have a certain 'fill'. The saturation model implies that local richness is restricted to an upper bound akin to the carrying capacity of the community. This leads to a situation, however, that in some simulations a species' range could be very different from what is observed in the natural environment, a factor that is modelled by the distribution constraint. The distribution model thus attempts to capture the effects of interspecific differences in dispersal and occurrence probabilities across sites. The doubly-constrained model incorporates both saturation and distribution effects by retaining row and column sums constant and such a model with both constraints has been considered by Stone *et al*. (1996) as necessary "to preserve a semblance of biological realism".

However, as Stone *et al*. (1996) point out this model does not preserve species geographical ranges as even if the number of occurrences are fixed, some occurrences would occur well beyond the species' known range. In the present case, this would produce substantial changes in the elevational range of species in simulations. As far as I am aware, this problem has not been surmounted and no modelling solution has been hitherto proposed that incorporates all these constraints. I therefore incorporated this additional constraint in the range-contiguity model, which retains the elevational range and contiguity of species, but locates it randomly. Some species in the data set were absent at a few intermediate sites in their elevational range possibly due to biotic or sampling effects. The number of such 'holes' in the distribution range was retained in the contiguity model but their location was randomised. I checked whether the matrix was so constrained as to be identical with the original

matrix, the so-called 'Narcissus effect' (Colwell and Winkler 1984, Wilson 1995), by determining the number of unique matrices possible in 5000 runs. I established that over 5000 different matrices existed, and thus the range-contiguity model may be confidently used to assess whether the observed pattern of similarities between sites could emerge from the constrained distribution of bird species independently of each other.

4.4 RESULTS

4.4.1 Bird species richness, diversity, and abundance

Across the 14 sites, I obtained over 2900 detections comprising approximately 6600 individuals of birds belonging to 67 species. Of these, nine species were latitudinal (winter) migrants and the remaining were resident species. Despite relatively intense sampling over the elevational gradient, 13 species were represented in the data set by a single detection and a further seven species were seen less than five times overall.

Total bird species richness (cumulative list in each site) was significantly negatively correlated to elevation of the site (Kendall rank-order correlation, $\tau = -0.52$, $df = 12$, $P = 0.01$, Table 4.1). Resident bird species richness appeared to decline with elevation, but this trend was not highly significant statistically ($P = 0.08$). The standardised estimates for 17 point counts obtained over 100 runs (sampling with replacement) of species richness, Shannon-Weiner diversity, Coleman rarefaction richness, bootstrap richness, and the Chao1 richness were all significantly negatively correlated to elevation ($P < 0.05$, Table 4.1). Bird abundance showed a converse positive association with elevation that was marginally significant ($\tau = 0.39$, $df = 12$, $P = 0.055$, Table 4.1).

The relationships between elevation and total bird species richness, resident bird species richness, and rarefaction bird species richness are illustrated in Figure 4.1. The pattern of decrease in species richness with elevation appears non-linear, with most of the decrease occurring between 500 and 900 m elevation, after which there is little change in species richness (Figure 4.1). For the above species richness measures, a slight U-shaped quadratic model gave marginally better fits ($R^2 = 0.59 – 0.82$) to the data than a linear model ($R^2 = 0.33 – 0.62$).

The estimates of bird species richness and abundance per point showed similar variation and trends with elevation. The total and resident bird species richness, detections, and abundance per point showed significant variation across the 14 sites (one-way ANOVA, $F_{13,329} > 5.58$, $P < 0.004$). Whereas total species richness and detections per point showed weak negative correlations with elevation, the trends for resident species richness and detections with elevation were non-significant (Table 4.1). These measures showed, however, a U-shaped quadratic relationship with elevation (results not presented here) as in the cases above. Bird abundance per point increased with elevation, weakly and non-significantly in the case of total abundance and significantly in the case of abundance of resident species (Table 4.1).

Table 1. Bird community parameters along an altitudinal gradient in the rainforests of Kalakad-Mundanthurai Tiger Reserve

Transect No.	T11	T12	T13	T14	T1	T2	T3	T9	T8	T10	T4	T5	T7	T6	Kendall rank correlations		
Transect Code	A	B	C	D	E	F	G	H	I	J	K	L	M	N	with altitude		
Mean altitude (m)	558	646	751	843	900	980	1092	1228	1256	1259	1265	1287	1341	1359	Tau	Z	*P*
Cumulative species richness																	
Total species	40	36	36	34	30	29	31	29	32	31	30	25	28	32	-0.520	-2.59	0.0096
Resident species	35	30	30	29	26	25	27	26	30	27	28	25	25	30	-0.352	-1.75	0.0798
Standardised for 17 point counts (EstimateS program)																	
Bird species richness	36.8	33.0	33.0	31.1	27.4	25.9	28.2	27.0	28.9	27.5	26.3	21.9	27.6	29.97	-0.407	-2.03	0.0428
SD	1.60	1.46	1.60	1.34	1.55	1.99	1.38	1.31	1.37	1.83	1.90	1.72	0.60	1.15			
Bird abundance (individuals/ha)	22.6	24.3	21.7	22.3	23.0	17.0	22.1	29.7	24.8	25.5	20.7	25.2	25.8	30.5	0.385	1.92	0.0554
SD	0.81	1.10	1.20	1.18	1.64	1.51	1.61	1.50	1.63	1.58	1.48	2.15	0.68	1.93			
Shannon-Weiner diversity	3.22	3.03	3.06	3.02	2.73	2.74	2.82	2.69	2.79	2.63	2.48	2.07	2.53	2.8	-0.626	-3.12	0.0018
SD	0.04	0.04	0.05	0.04	0.08	0.08	0.05	0.07	0.06	0.07	0.11	0.09	0.03	0.05			
Coleman rarefaction richness	37.7	34.1	34.2	32.3	28.5	27.8	29.8	28.1	31.4	29.1	27.9	23.4	27.8	31.3	-0.538	-2.68	0.0073
SD	1.29	1.18	1.16	1.14	1.06	0.99	0.96	0.84	0.72	1.23	1.25	1.10	0.41	0.76			
Bootstrap richness	41.1	37.1	37.3	34.3	30.8	29.6	31.5	29.8	32.3	31.2	30.4	25.2	30.5	33.1	-0.429	-2.14	0.0328
SD	2.11	1.92	2.15	1.79	1.98	2.45	1.80	1.71	1.86	2.42	2.46	2.19	0.76	1.42			
Chao1 richness	40.6	33.9	35.1	32.1	28.3	26.2	28.5	27.2	29.0	28.3	28.3	23.6	28.3	30.2	-0.420	-2.09	0.0365
SD	6.31	2.06	4.38	2.08	2.20	0.86	1.19	0.19	0.46	1.60	3.70	4.38	2.08	1.00			
Values estimated per point																	
All species	8.8	8.5	8.4	8.3	6.3	5.5	7.4	8.7	7.4	7.4	6.1	6.2	7.4	8.4	-0.331	-1.65	0.0986
SE	0.48	0.34	0.47	0.53	0.46	0.57	0.47	0.43	0.67	0.50	0.51	0.62	0.65	0.52			
Detections	9.9	9.8	9.8	9.4	7.0	6.7	8.9	9.8	7.6	8.2	6.6	7.1	7.6	9.2	-0.407	-2.03	0.0428
SE	0.55	0.45	0.57	0.59	0.47	0.65	0.63	0.50	0.71	0.55	0.55	0.75	0.69	0.58			
Individuals	17.6	18.8	17.0	17.5	17.8	13.4	17.5	23.2	19.6	20.1	16.2	20.0	20.1	23.9	0.376	1.87	0.0613
SE	1.06	1.25	1.39	1.37	1.91	1.57	1.84	1.60	2.00	1.85	1.60	2.43	2.17	2.15			
Resident species	7.4	6.8	6.5	7.0	5.8	4.9	6.3	8.1	6.7	7.0	6.0	6.2	6.7	8.0	-0.033	-0.16	0.8695
SE	0.49	0.31	0.44	0.51	0.45	0.42	0.41	0.39	0.56	0.44	0.51	0.62	0.55	0.50			
Resident detections	8.3	7.8	7.4	7.9	6.4	5.9	7.5	9.2	6.9	7.8	6.6	7.1	6.8	8.8	-0.110	-0.55	0.5820
SE	0.56	0.36	0.48	0.55	0.46	0.43	0.58	0.46	0.62	0.49	0.56	0.75	0.59	0.56			
Resident individuals	16.0	16.8	14.6	16.0	17.2	12.6	16.2	22.6	18.9	19.7	16.2	20.0	19.3	23.5	0.522	2.60	0.0093
SE	1.08	1.25	1.31	1.40	1.96	1.38	1.80	1.58	1.92	1.84	1.61	2.43	2.15	2.11			

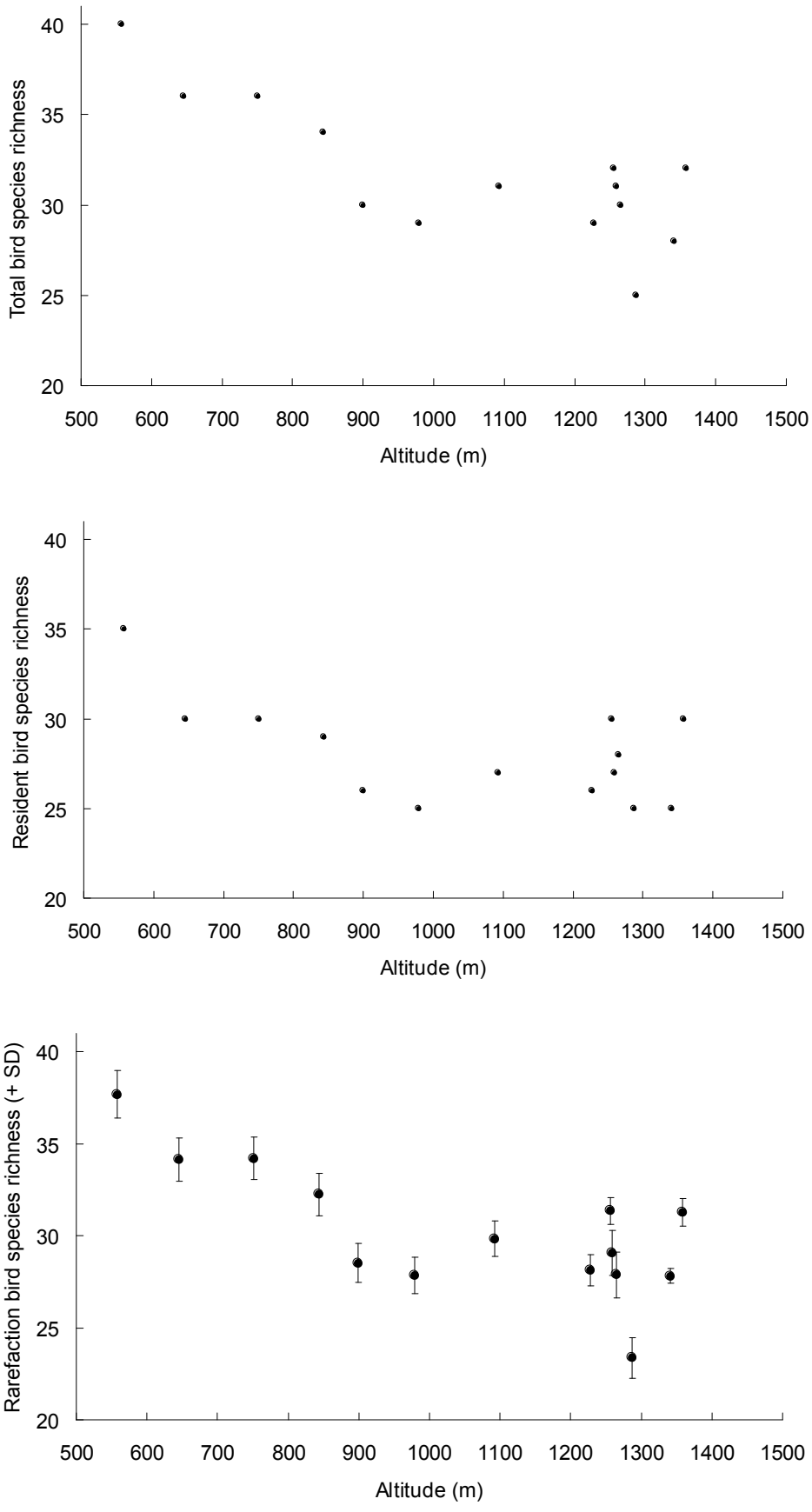

Figure 4.1: Variation in bird species richness with elevation in the tropical rainforests of Kalakad-Mundanthurai Tiger Reserve; (a) upper panel: total species richness, (b) middle panel: species richness of residents, (c) lower panel: Coleman rarefaction species richness (vertical bars are 1 SD).

4.4.2 Diet-guilds

The number of species of canopy, understorey, and terrestrial insectivores increased significantly with elevation ($\tau > 0.41$, $df = 12$, $P < 0.05$). In contrast, the species richness of frugivores and omnivores decreased with elevation ($P < 0.005$). There was no significant relationship between the number of species in the carnivore, nectarivore-insectivore, and bark-surface feeder guilds and elevation, although species richness of bark-surface feeders appeared to be slightly higher in mid-elevations (Table 4.2). When all three insectivore guilds were combined, total insectivore species richness was found to increase with elevation ($\tau = 0.62$, $P = 0.002$).

The abundance of birds belonging to different diet-guilds also showed substantial variation along the elevational gradient (Table 4.2). The abundance of birds in different diet-guilds was significantly different across sites (one-way ANOVA, $F_{13,329} > 2.73$, $P \leq 0.001$) except in the case of bark-surface feeders ($F_{13,329} = 1.35$, $P = 0.29$). Whereas canopy and understorey insectivore abundance increased with elevation as in the case of species richness, there was no significant correlation between elevation and abundance of terrestrial insectivores (Table 4.2). Again, frugivore and omnivore abundance was significantly negatively correlated to elevation as in the case of their species richness, but nectarivore-insectivore abundance was strongly positively correlated to elevation despite a significant decrease in species richness. Abundances of carnivores and bark-surface feeders were not significantly correlated to elevation (Table 4.2). Abundance of all insectivores (terrestrial, understorey, and canopy) combined also increased with elevation ($\tau = 0.71$, $P < 0.001$).

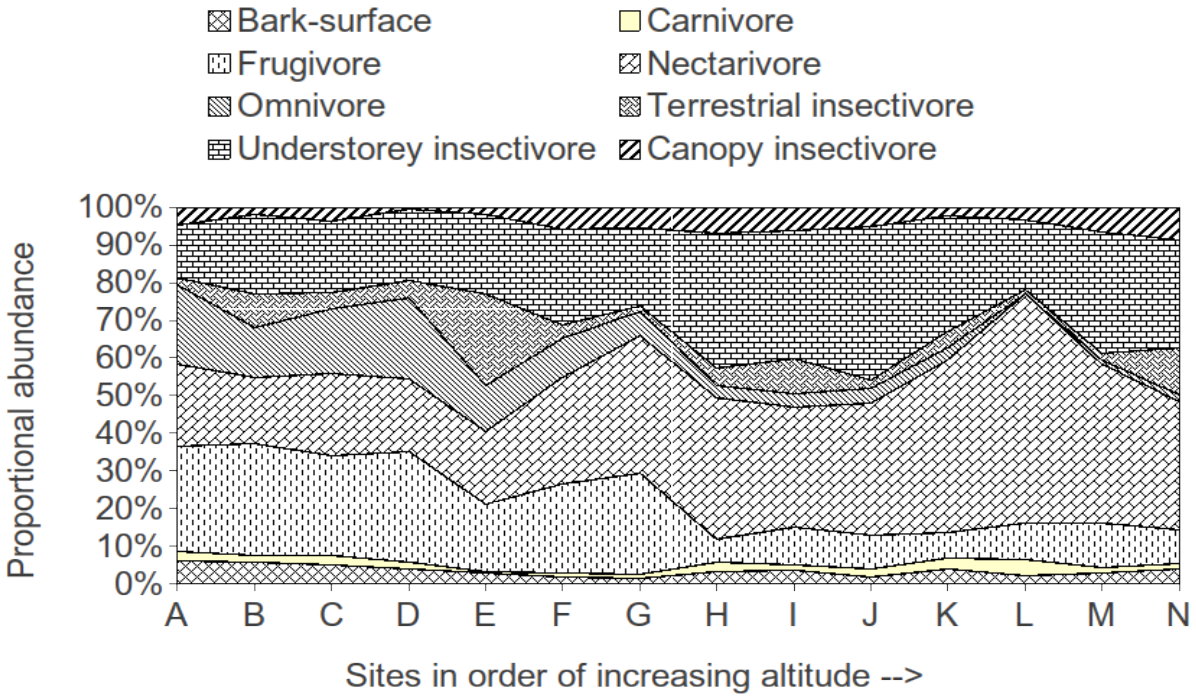

Figure 4.2: Changes in the proportional abundance of birds in different diet-guilds along the elevational gradient in the rainforests of KMTR. Sites are named A to N in increasing order of elevation.

Table 2. Species richness and abundance of birds in different guilds along the altitudinal gradient in rainforests of KMTR

Transect No.	T11	T12	T13	T14	T1	T2	T3	T9	T8	T10	T4	T5	T7	T6	Kendall rank correlations		
Transect Code	A	B	C	D	E	F	G	H	I	J	K	L	M	N	with altitude		
Mean altitude (m)	558	646	751	843	900	980	1092	1228	1256	1259	1265	1287	1341	1359	Tau	Z	*P*
Species richness																	
Bark-surface feeders	3	3	4	5	5	5	5	5	5	5	4	3	3	3	-0.123	-0.61	0.5406
Carnivores	3	3	3	3	3	3	3	3	3	3	4	2	2	3	-0.195	-0.97	0.3315
Frugivores	9	8	8	8	6	5	5	4	4	4	4	4	5	4	-0.752	-3.75	0.0002
Nectarivore-insectivores	7	6	6	6	6	5	5	5	5	5	5	5	4	4	-0.832	-4.15	0.0000
Omnivores	6	5	7	7	7	7	7	5	5	5	5	4	4	4	-0.610	-3.04	0.0024
Terrestrial insectivores	2	2	3	3	3	3	3	3	4	5	4	4	4	4	0.741	3.69	0.0002
Understorey Insectivores	5	5	5	5	5	5	6	6	6	6	6	6	6	6	0.726	3.62	0.0003
Canopy insectivores	2	1	1	1	1	2	2	4	4	4	4	4	4	3	0.602	3.00	0.0027
Abundance (individuals/ha)																	
Bark-surface feeders	1.27	1.27	0.97	0.81	0.66	0.31	0.31	0.97	0.92	0.51	0.87	0.56	0.71	1.22	-0.223	-1.11	0.2655
SE	0.33	0.39	0.32	0.32	0.29	0.17	0.22	0.27	0.29	0.21	0.31	0.26	0.34	0.39			
Carnivores	0.51	0.36	0.46	0.36	0.05	0.15	0.25	0.76	0.31	0.51	0.56	1.12	0.35	0.41	0.167	0.83	0.4063
SE	0.16	0.14	0.12	0.14	0.05	0.08	0.10	0.18	0.11	0.13	0.17	0.17	0.14	0.12			
Frugivores	5.65	6.32	4.89	6.01	3.97	3.82	5.50	1.73	2.39	2.24	1.38	2.44	2.90	2.65	-0.516	-2.57	0.0101
SE	0.80	0.71	0.59	0.71	0.47	0.51	0.58	0.40	0.44	0.49	0.28	0.42	0.62	0.60			
Nectarivore-insectivores	4.43	3.77	3.97	3.97	4.18	4.53	7.49	10.75	7.69	8.76	9.42	15.43	10.40	10.19	0.729	3.63	0.0003
SE	0.50	0.50	0.38	0.34	0.49	0.78	1.32	1.30	1.37	1.52	1.53	2.08	1.99	1.40			
Omnivores	4.23	2.80	3.16	4.38	2.70	1.63	1.32	1.02	0.87	1.02	0.66	0.05	0.21	0.56	-0.818	-4.07	0.0000
SE	0.65	0.56	0.60	0.73	0.59	0.55	0.32	0.33	0.27	0.30	0.29	0.05	0.15	0.23			
Terrestrial insectivores	0.36	1.94	0.81	0.92	5.30	0.56	0.31	1.32	2.24	0.56	0.87	0.25	0.50	3.72	-0.044	-0.22	0.8257
SE	0.20	1.00	0.23	0.26	1.91	0.22	0.15	0.78	0.86	0.17	0.23	0.15	0.26	1.35			
Understorey Insectivores	2.85	4.48	3.51	3.87	4.63	4.07	4.28	10.29	8.15	10.19	6.37	4.74	7.85	8.56	0.560	2.79	0.0052
SE	0.66	1.12	0.96	0.82	0.83	0.86	0.94	1.18	1.24	1.18	0.84	0.92	1.11	0.91			
Canopy insectivores	0.97	0.41	0.66	0.10	0.41	0.97	1.12	1.99	1.53	1.27	0.46	0.87	1.63	2.60	0.456	2.27	0.0232
SE	0.40	0.23	0.38	0.10	0.32	0.54	0.51	0.48	0.54	0.40	0.26	0.45	0.55	0.47			

The proportional representation of birds of different diet-guilds therefore varied substantially with elevation (Figure 4.2). Nectarivore-insectivores comprised only 18–22% of total bird abundance below 900 m but contributed to 28–61% of total birds above 900 m. The proportion of frugivorous birds declined from around 30% at the lower end of the elevational gradient to a third as much at the upper end. Omnivores, averaging 17% of all birds in the three lowest elevation sites, contributed to only 1% of total birds in the three highest sites. The corresponding values for canopy insectivores were 2% and 6%, respectively. Interestingly, terrestrial insectivore abundance showed a multimodal pattern being high at both ends of the gradient and at around 900 and 1250 m (Table 4.2, Figure 4.2). The correlations of diet-guild proportions with elevation were virtually identical to those obtained using abundances (results not presented here).

4.4.3 Vegetation

I examined changes in vegetation attributes with elevation across the 14 rainforest sites as a prelude to looking for possible correlations with bird community changes (Figure 4.3). In contrast to the clear patterns of variation in bird community attributes, vegetation variables showed little or no consistent trends of variation with elevation. The vegetation parameters were not significantly correlated with elevation (Kendall correlations, $P > 0.05$). The only exception was bamboo culm density that was positively correlated with elevation ($\tau = 0.52$, $df = 12$, $P = 0.01$) mainly due to the occurrence of bamboo at only two higher elevation sites (Figure 4.3). Bamboo density along with cane and shrub density showed much greater variation across sites than the other variables that spanned a more limited range of values.

The six standardised estimates of bird species richness (see Methods), Shannon-Weiner bird diversity, and the per-point total and resident bird species richness were all significantly negatively correlated to one of the vegetation variables: leaf-litter depth ($\tau < –0.45$, $df = 12$, $P < 0.03$ in all cases). These variables were also not correlated to any of the other vegetation variables. Bird abundance (standardised and per-point) and the total number of bird detections per point were not correlated to any vegetation variable. The average number of resident bird detections per point was, however, negatively correlated to leaf litter depth ($\tau = –0.47$, $P = 0.037$).

4.4.4 Range distributions, sizes, and species richness

The range size and distribution pattern across the 58 resident bird species varied from species occurring from one to all the 14 sampled sites spanning the entire gradient. Among species that occurred in the same site or number of sites, there were considerable differences in population densities and spatial trends in densities (Appendix 2). Twenty-three species (39.7%) were either restricted to lower elevations or showed declining trends with elevation in population density (Kendall correlations, $P < 0.10$, Appendix 2). Sixteen species (27.6%) displayed a trend of increase in

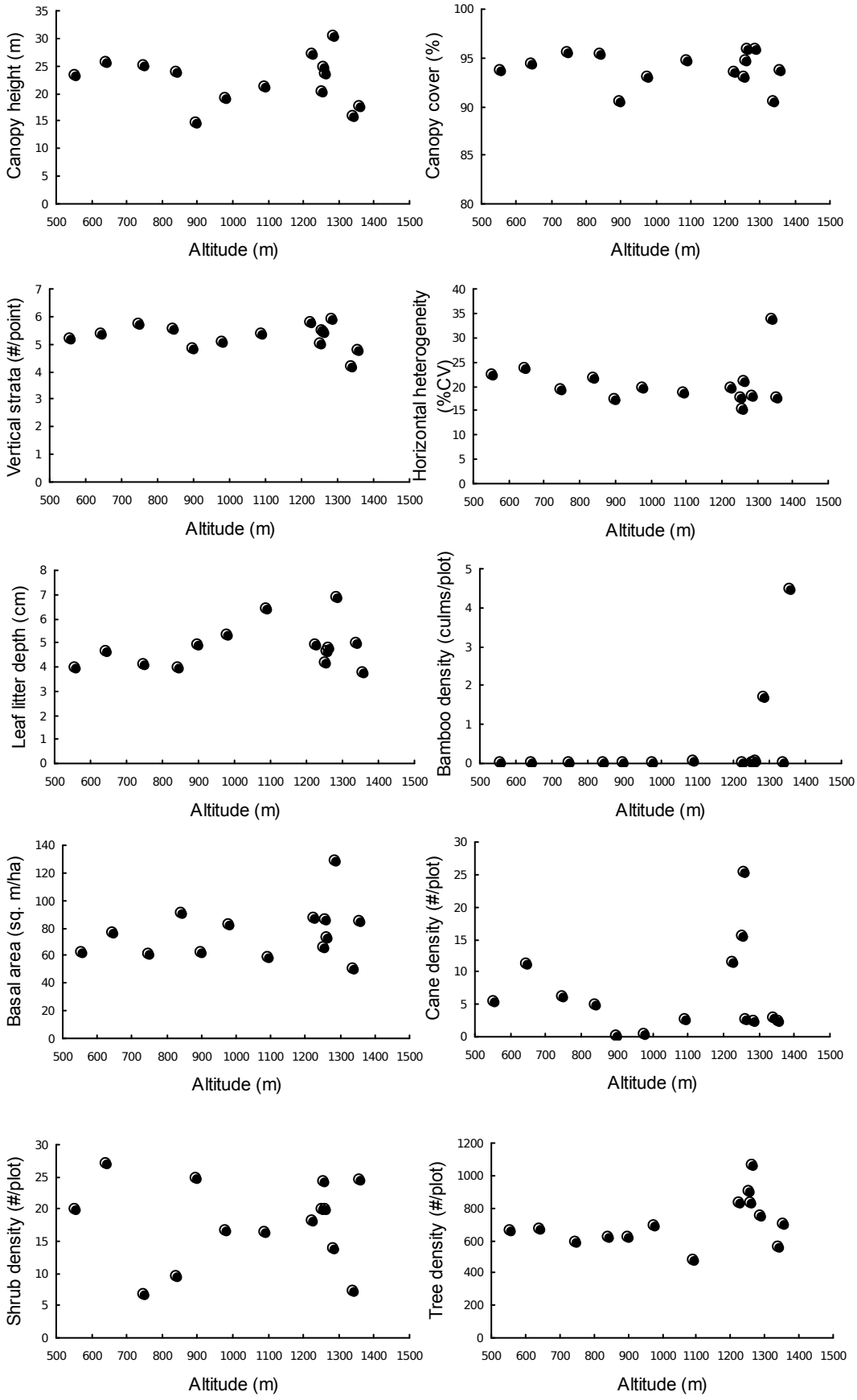

Figure 4.3: Variation in vegetation variables with elevation in the rainforests of KMTR.

population density with elevation ($P < 0.10$) or were restricted largely to higher elevation sites (Appendix 2). Only two species of woodpeckers, Common Flameback and White-bellied Woodpecker, appeared to be restricted to mid-elevations. The spatial distributions of the remaining species were widespread and relatively uniform (14 species) or could not be determined due to low sample sizes (3 species).

The patterns of distribution of species and range sizes in turn influenced the observed species richness along the elevational gradient. The elevational gradient from 500 to 1,400 m was divided into 18 zones of 50 m elevation width. The number of resident bird species whose elevational ranges intercepted each zone was nearly constant at around 35 species (Figure 4.4a). This was contrary to the predictions of the Veech (2000) null model that simulated random placement of observed elevational range widths on the gradient. The null model predicted an inverse U-shaped species richness curve peaking in the middle of the gradient (mid-domain effect, Figure 4.4a), which was accurately described by a polynomial model ($y = –0.0001\ x^2 + 0.2027\ x – 53.065$, $R^2 = 0.99$). The observed displacement ($d = 6.51$) of the species richness curve from the composite average null curve was highly significantly different from the displacement expected under the null model (1000 simulations, $P < 0.001$).

The relationship between elevational range size of a species and the weighted midpoint of its elevational range was also non-linear and quadratic (Figure 4.4b, fitted curve: $y = –0.0046\ x^2 + 8.8633\ x – 3496.8$, $R^2 = 0.72$). Similarly, in contrast to the expectation under Rapoport's rule, the mean elevational range of species in each site showed a quadratic relationship with the elevation of the site (Figure 4.4c, fitted curve: $y = –0.0005\ x^2 + 8.8839\ x + 216.99$, $R^2 = 0.78$).

To examine whether more abundant species also had wider ranges, species elevational range size was related to two measures of density: (i) ecological density, D_{eco}, calculated as the average across all sites where a species occurred, and (iii) maximum density achieved in any site, D_{max}. Figure 4.5 shows non-linear, allometric relationships between elevational range and ecological density ($y = 530.7\ D_{eco}^{0.42}$, $R^2 = 0.22$) and maximum density ($y = 435.3\ D_{max}^{0.44}$, $R^2 = 0.33$). As can be seen from the R^2 values, these relationships were weak and there was considerable interspecific variation.

4.4.5 Bird community similarity between sites

Species turnover was considerable along the elevational gradient (Appendix). Non-metric multidimensional scaling ordination using the Morisita dissimilarity matrix of the data on tree and bird species composition showed similar patterns (stress = 0.070 and 0.034, Figure 4.6a-b, respectively). Sites below 900 m tended to cluster together as did sites above 1,100 m, while intermediate sites were relatively dissimilar to the others. The exception to this pattern was shown in tree species composition by site D (average elevation 843 m) that was linked to site G (1,092 m)

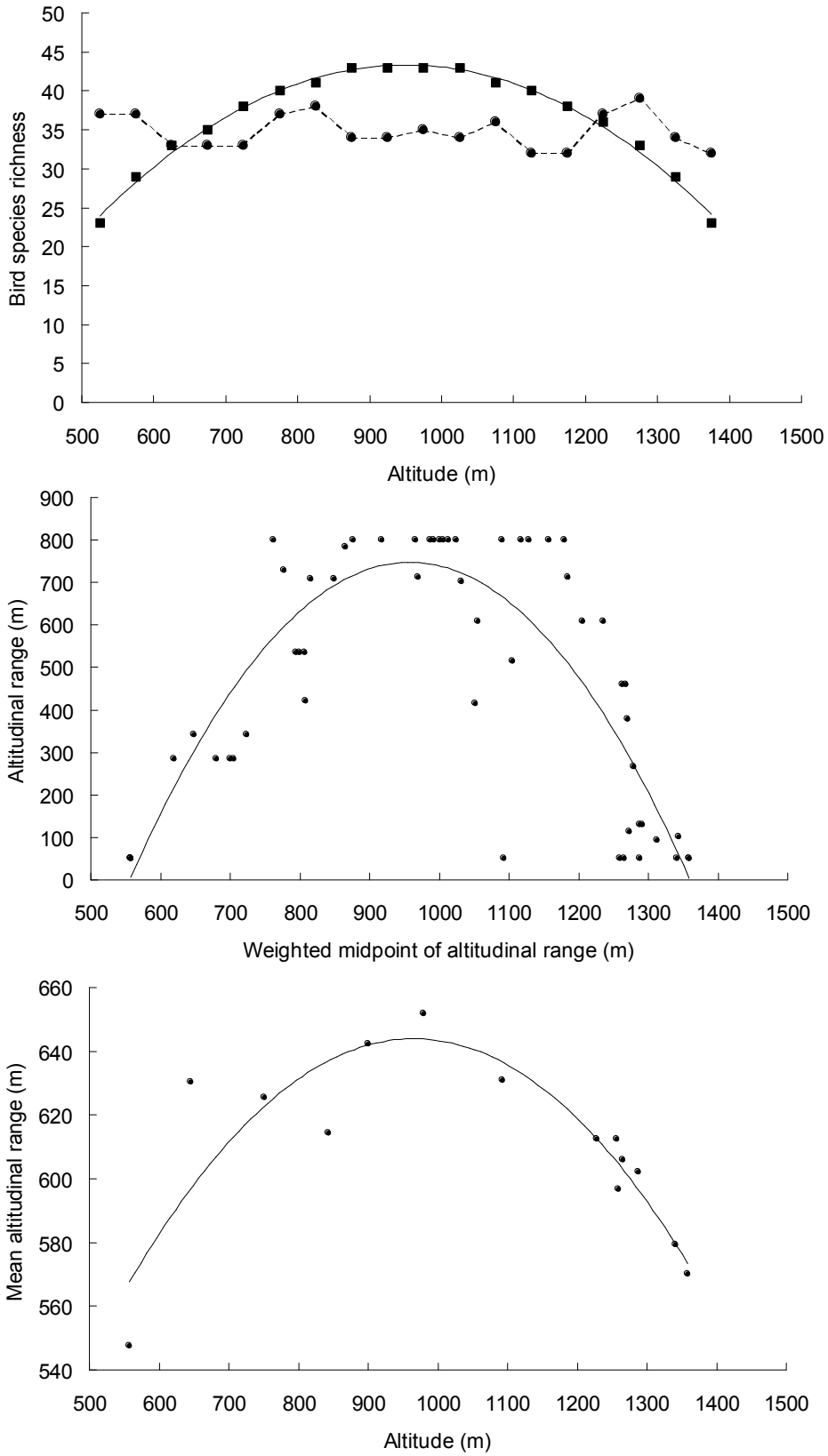

Figure 4.4: Bird species richness and range size relationships in rainforests of KMTR; (a) upper panel: evaluation of the Veech (2000) null model of the mid-domain effect—line shows best fit curve to null model estimates whereas the dotted line shows observed curve; (b) middle panel: elevational range size of resident bird species in relation to the weighted mid-point of their elevational range; and (c) lower panel: mean elevational range of species at each of the 14 sampled sites in relation to elevation of the sites.

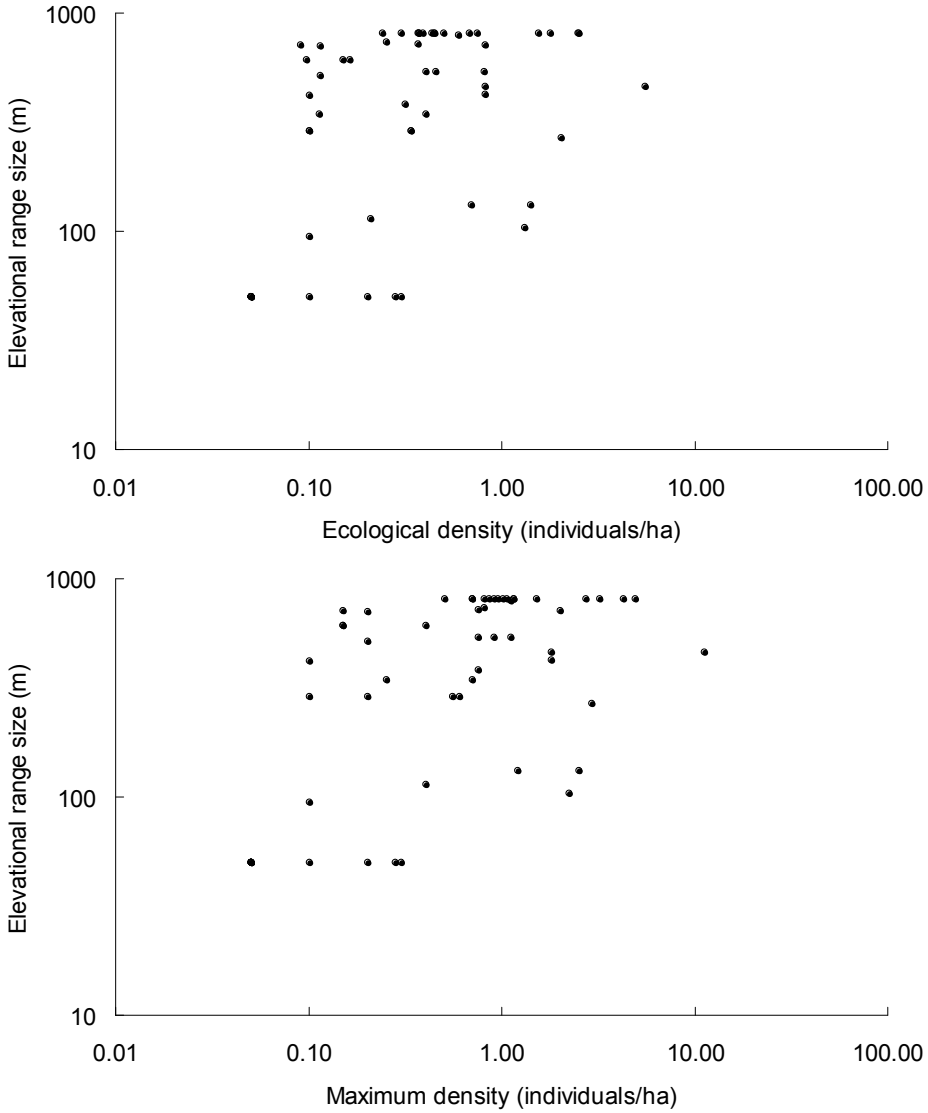

Figure 4.5: Relationships between elevational range sizes of resident bird species and (a) ecological density (upper panel) and (b) maximum density at any site (lower panel) in the rainforests of KMTR.

rather than the other lower elevation sites, and site M (1,341 m) that was relatively dissimilar to the sites in the high altitude cluster.

Mantel tests indicated that dissimilarity in bird community composition between sites was significantly positively correlated to elevational distance ($P < 0.0001$, Figure 4.7a) and dissimilarity in tree species composition between sites ($P < 0.0001$, Figure 4.7b). These two independent variables were themselves positively correlated ($P < 0.0001$). Dissimilarity in foliage profile was not strongly related to bird community composition ($P = 0.101$, Figure 4.8c) or elevational distance ($P = 0.81$), although it was positively correlated to tree species compositional similarity ($P = 0.043$). Geographic distance between sites was correlated to elevational distance between sites ($P = 0.0012$), dissimilarity in bird species composition ($P = 0.0022$), and dissimilarity in tree species composition ($P = 0.0061$).

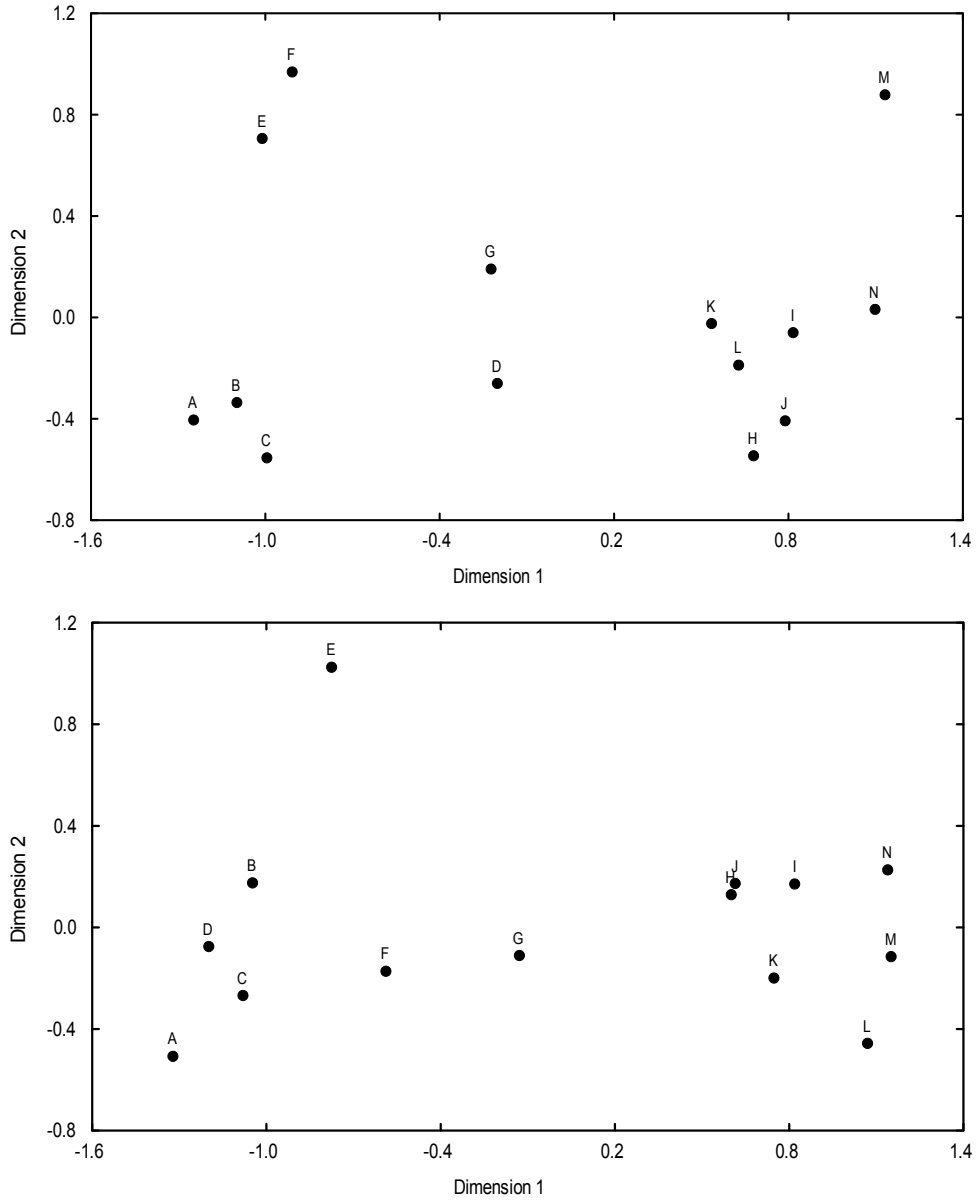

Figure 4.6: Ordination of study sites on the basis of similarity in (a) tree species composition (upper panel) and (b) bird community composition (lower panel) using multidimensional scaling. Sites are named A to N in increasing order of elevation.

Since the independent variables correlated to bird community composition were themselves inter-correlated, I used partial Mantel tests to assess the significance of each, controlling for the other. I found that dissimilarity in bird community composition between sites was independently positively correlated to both elevational distance between sites ($T = 0.60$, $P < 0.0001$) and dissimilarity in tree species composition ($T = 0.22$, $P = 0.013$). Correlations with both these variables were significant even when the effects of geographic distance were controlled for ($T = 0.69$ and 0.51, $P < 0.0003$). In contrast, geographic distance between sites had no effect on bird species composition, when the effects of elevational distance were controlled for ($T = 0.08$, $P = 0.12$), indicating the primary importance of elevation.

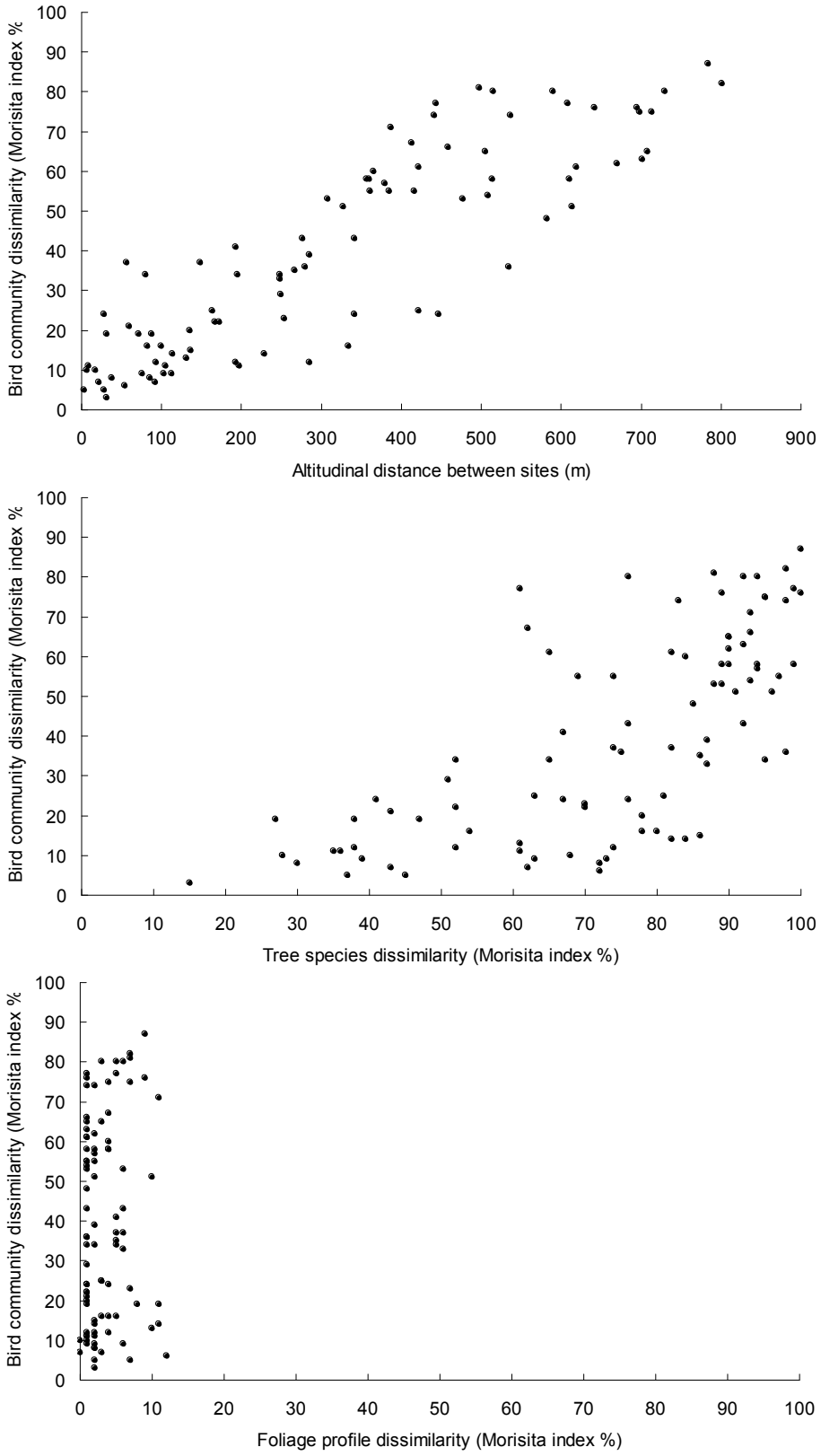
Bird community dissimilarity (Morisita index %
Altitudinal distance between sites (m)
Bird community dissimilarity (Morisita index %
Tree species dissimilarity (Morisita index %)
Bird community dissimilarity (Morisita index %
Foliage profile dissimilarity (Morisita index %)

Figure 4.7: Bird community dissimilarity between sites (91 all possible pairwise comparisons) in relation to corresponding between-site (a) elevational distance (upper panel), (b) tree species dissimilarity (middle panel), and (c) foliage profile dissimilarity (lower panel). Sites that were separated by greater elevational distances or that were more dissimilar in their tree community differed more in the bird community composition.

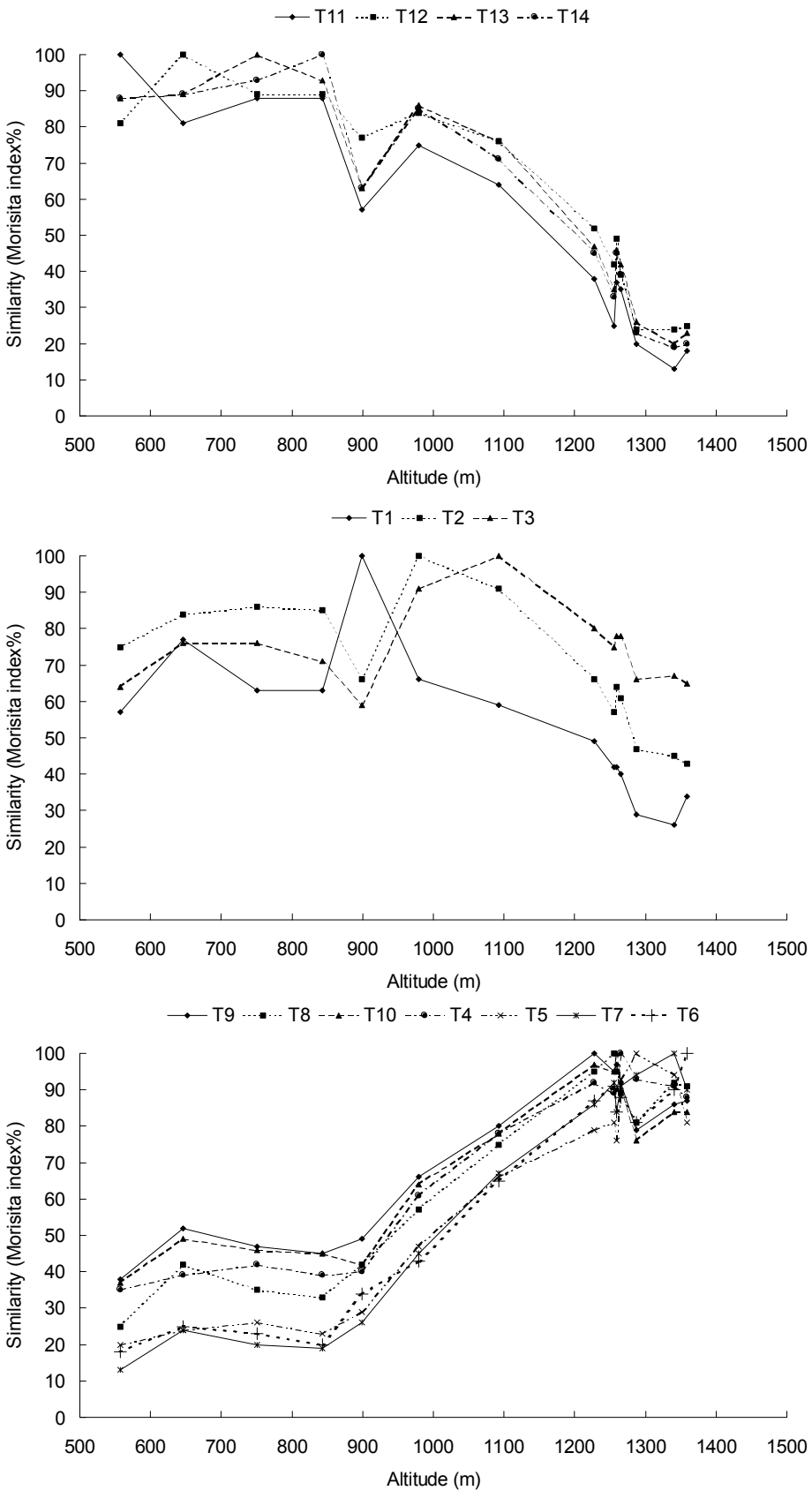

Figure 4.8: The 'faunal congruity' curves of Terborgh (1971) applied to rainforest bird communities in KMTR. Each line depicts similarity between one site and other sites as a function of elevation. All curves peak at 100% similarity at the corresponding site's elevation as a site was assumed to be 100% similar to itself. (a) upper panel: data from four lower-elevation sites, (b) middle panel: three mid-elevation sites, and (c) lower panel: six higher-elevation sites.

4.4.6 Pattern of species turnover

The similarities in bird community composition (Morisita index) of each site with other sites is illustrated in Figure 4.8(a–c) assuming 100% similarity of a site with itself. The four lowest sites (below 900 m) had highly similar (c. 90%) bird community composition (Figure 4.8a). There appeared to be one major transition zone around 900 m elevation, beyond which community composition changed relatively continuously and consistently with elevation (Figure 4.8b–c).

Species turnover between sites (average calculated through comparisons of the 91 possible pairs) was 0.529 ± 0.139 SD using the Jaccard index and 0.608 ± 0.251 SD by the Morisita index. The average species turnover between successive sites (13 comparisons) along the elevational gradient was lower than the turnover between all possible pairs. This was reflected in the higher average

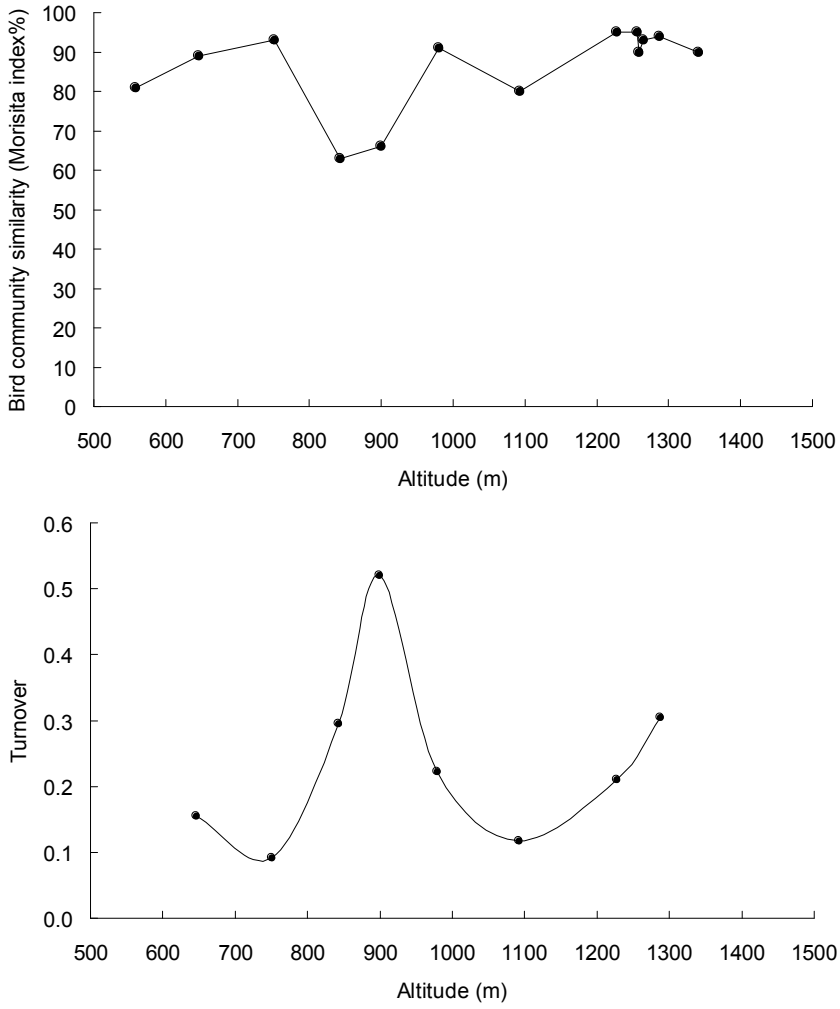

Figure 4.9: Turnover in rainforest bird community composition as a function of elevation in KMTR. In the upper panel (a) similarity between each site and the immediately higher site is plotted against elevation of the lower site. The lower panel (b) uses data from 10 roughly equally-spaced sites along the gradient and plots rate of change in similarity between a site and the sites immediately lower and higher to it against elevation of the central site. The rate of change of similarity was calculated as $\frac{1}{2}[(d_1/w_1)+(d_2/w_2)]$, where d_1 and w_1 are the Morisita index dissimilarity and elevational distance between a site and the lower site, and d_2 and w_2 the corresponding values for the higher site.

similarity between adjacent sites of 0.693 ± 0.107 SE using the Jaccard index and 0.860 ± 0.103 SE by the Morisita index. The pattern of turnover was not monotonic or increasing with elevation, and remained relatively low but for higher turnover (lower similarity) around 1,000 m (Figure 4.9).

4.4.7 Null models of species turnover

I assessed whether the five null models of bird species turnover could accurately estimate the observed Jaccard similarity between all possible pairs of sites (0.529 ± 0.139 SD) and between adjacent pairs of sites (0.608 ± 0.107 SD). The results are compared in Figure 4.10.

The unconstrained model and saturation models gave similar results, producing similarity estimates that were significantly lower than observed ($P < 0.0002$, Figure 4.10). The estimated average similarities between all possible pairs of sites by the range-contiguity model and the doubly constrained model were remarkably close to that actually observed (0.516 *vs.* 0.529) but was, nevertheless, significantly lower ($P < 0.0002$). The double-constraint model also performed poorly in estimating average similarity between adjacent sites (0.517 *vs.* 0.693). The range-contiguity model estimated similarities between adjacent sites that were higher and much closer to the observed value (0.622 *vs.* 0.693). However, the model estimates were significantly lower than the observed values for both the double-constrained and range contiguity models ($P < 0.0002$, Figure 4.10).

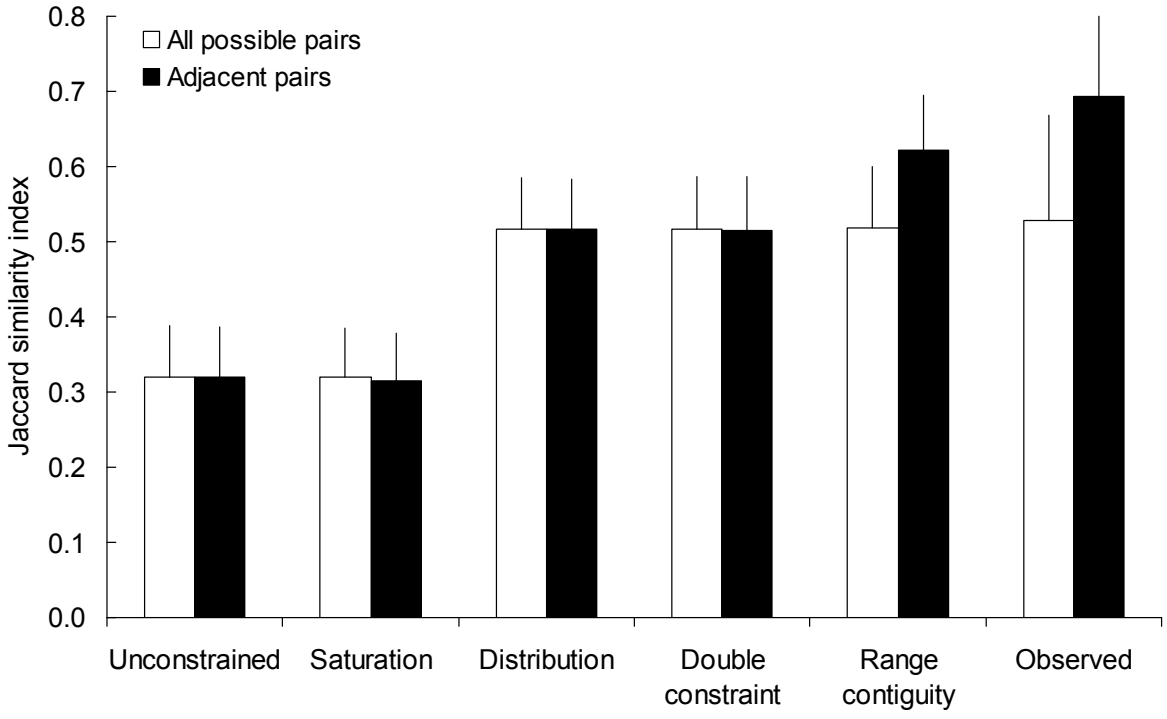

Figure 4.10: Between-site similarities (average Jaccard index) in rainforest bird community composition estimated from the five non-equilibrium null models compared with observed values in the data set. Open bars—average similarity between all possible pairs, filled bars—average similarity between adjacent pairs. Vertical lines are 1 SD.

4.5 DISCUSSION

4.5.1 Species richness

A clear pattern emerging from this study is that species richness of resident rainforest birds varies little, despite substantial change in community composition, across the elevational gradient. This pattern is in contrast to the four main models hitherto proposed to describe variation in species richness with elevation (Rahbek 1997). The general model, propounding a monotonous decline in species richness with elevation in parallel with an assumed decline in productivity, finds weak support, if any, in this study, when all bird species including latitudinal migrants are considered. The greater tendency for migrants, which were all insectivorous birds, to occur at lower elevations contrasted with the pattern of increase with elevation in resident insectivorous bird species richness in this study. Rahbek (1997) also indicates that a monotonous decline in species richness with elevation can occur under Rapoport's rule. It has since been shown that this is true only when other highly specific ecological conditions (competition, rescue-effect) also operate (Taylor and Gaines 1999). In any case, the pattern of rainforest bird range sizes observed in this study results in species richness patterns that depart significantly from expectations under Rapoport's rule, hump-shaped relationships with productivity (Rosenzweig and Abramsky 1995), or mid-elevation peaks arising from geometric constraints (the mid-domain effect, Colwell and Lees 2000).

In contrast, the observed pattern of bird species richness is a spatial analogue to the recent theoretical model proposed by Brown *et al*. (2001) to explain the regulation of local species richness over time in changing environments. Brown *et al*. (2001) suggest that species composition may vary substantially over time, but species richness, as an emergent property of ecosystems, is often regulated within narrow limits. Five conditions are necessary and sufficient for this to occur: (i) productivity, or resource availability, remains relatively constant, (ii) other abiotic or biotic factors vary, causing turnover in species composition, (iii) a regional species pool provides a source of colonists to local sites that are open systems with respect to species colonisation and extinction, (iv) the species pool contains species capable of utilizing the entire range of resources and showing compensatory shifts in abundance, and (v) the division rule governing apportioning of resources across species results in similar ranked species-abundance distributions (Brown *et al*. 2001).

The data provide partial support for the applicability of these criteria for rainforest birds in KMTR. Although productivity could not be directly measured, the relative constancy or lack of clinal change in rainforest vegetation variables across the elevational gradient suggests that habitat structure and resource availability for rainforest birds did not vary substantially. This is partly due to the elevational gradient sampled in this study (500-1,400 m) being narrower than in other studies from the Neotropics (Terborgh 1971, 1977, Rahbek 1997). Where a wider range is considered and vegetation shows substantial directional change along the elevational gradient, bird diversity declines with

elevation and the corresponding reduction in forest structural complexity—as in the Peruvian Andes (Terborgh 1977). In the present study, bird species richness variables were uncorrelated to any vegetation variables except for a negative, possibly spurious, correlation with leaf litter depth. The second condition of Brown *et al*. (2001), species turnover due to changes in abiotic and biotic variables, finds clear support in the correlated variation in bird community composition in relation to elevation and tree species composition. The existence of a species pool that is nearly twice as large (with at least 58 species) as in any one local sampling site (around 30 species), provides evidence for the third criterion. Nevertheless, although local sites may represent systems open to colonization and extinction events, these events may not occur completely stochastically. Instead, the differences between species in range sizes, their greater likelihood of occurring at nearby elevations, and their elevational trends in abundance, make local composition more deterministic and the dynamic changes more circumscribed. Finally, the occurrence of a number of species that occurred across the entire elevational gradient and the similar overall bird abundance and ranked species-abundance distributions (data not presented here), suggest support for the final criteria. Further support is, however, required in the form of compensatory shifts in abundance of bird species along the elevational gradient in relation to occurrence of other species, particularly congeners, as noted in other studies of tropical forest birds (Terborgh 1971, Terborgh and Weske 1975).

On the other hand, analysis at the diet-guild level provides only partial support for the Brown *et al*. (2001) model as applied to spatial gradients. First, although change in guild structure (the number of species in the different diet-guilds) was minimal with even the extremes of the elevational gradient being nearly 90% similar (Morisita index) as seen in other bird community studies (MacNally 1994, Blake and Loiselle 2000), guild structure change was correlated to change in bird species composition. The regulation of guild structure over a narrow range of values suggests similar resource distribution (occurrence of main resource niches) across the elevational gradient. In contrast, the abundances of birds in the different guilds varied with elevation. An increase in nectarivore abundance and decline in frugivore abundance with elevation has been noted in other tropical forests (Terborgh 1977, Blake and Loiselle 2000). The increase in insectivore abundance with elevation noted here is, however, contrary to the pattern noted by Terborgh (1977). Changes in abundance may reflect changing resource abundance with elevation, decreasing support for explanations under the Brown *et al*. (2001) model. It is possible, however, that biomass or energy use by bird communities may be better indices of resource availability (Wiens 1989). In this study, biomass may have remained roughly constant with elevation. This is because the higher elevations were dominated by nectarivores and insectivores that tended to be of small body size (mainly Oriental White-Eye and Crimson-backed Sunbird). In contrast, frugivores and omnivores, that dominated in lower elevations tended to be larger birds (such as Malabar Grey Hornbill, White-bellied Treepie, and Asian Fairy Bluebird).

4.5.2 Species range sizes and distribution

Range sizes of rainforest birds at KMTR do not conform to the expectations under Rapoport's rule. This is not surprising considering recent work suggesting that the positive correlation between range size and elevation will appear only under specific ecological conditions including effects of competition and the rescue effect (Taylor and Gaines 1999). The failure of Rapoport's rule and the mid-domain effect, indicating that range sizes do not increase monotonically and are not located randomly with elevation, is primarily a consequence of the peculiar distribution pattern of rainforest birds in KMTR. A number of species, particularly those endemic to the Western Ghats, were restricted in distribution to lower (e.g. Malabar Grey Hornbill, White-bellied Blue Flycatcher) or higher (Black-and-Orange Flycatcher, White-bellied Shortwing) elevations (Appendix 2, Ali and Ripley 1983). Daniels (1992) has noted that a significant proportion of endemics, among birds and angiosperms in the Western Ghats, is restricted to the higher hills (> 1000 m). In other words, bird distributions were mainly of three types, restricted-range species of low and high elevations, and widely distributed species found at mid-elevations. In contrast, there were no species with small ranges that were located at the centre of the elevational gradient. The low elevation species included many that also use moist deciduous forest habitats (e.g., Malabar Grey Hornbill, Malabar Parakeet, Grey-headed Bulbul), whereas high-altitude restricted species are largely confined to wet evergreen rainforest (e.g., Black-and-Orange Flycatcher, White-bellied Shortwing, Nilgiri Flycatcher, Ali and Ripley 1983). This pattern may be a consequence of historical factors that influenced the prevalence and distribution of rainforest over geological time scales. It is possible that during drier climatic periods tropical rainforests were largely confined to montane regions and gave way to moist deciduous formations at lower elevations, triggering the evolution of restricted-range rainforest endemics that presently occur only in the higher altitudes and low-altitude endemics that also occur in moist deciduous forests. In the absence of palaeoecological data this is however only speculative.

Positive correlations between geographic range sizes and abundance have been noted in many macroecological community studies (Brown 1984, 1995, Wiens 1989). This paper presents evidence for a positive relationship, perhaps for the first time, between elevational range size and the ecological (or maximum) population density attained by rainforest bird species. As range size showed a quadratic relationship with range location on the elevational gradient, this also implied that species occurring at the centre of the elevational range tended to achieve higher densities than species that occurred towards either periphery of the gradient (500 or 1,400 m) beyond which very limited tropical rainforest habitat was available in the study area. Although this parallels the more commonly seen intraspecific pattern (Gaston 1990, Brown 1995), the interspecific differences suggest that species that enjoy substantial rainforest habitat above and below their range mid-point achieve higher population densities possibly due to the opportunities to maintain their populations in the face of environmental variation by movements or use of adjoining areas. On the other hand, species with their range mid-

points at mid-elevations, which represent a zone of turnover, may be more generalist in nature than typical low-elevation or montane birds, and thereby achieve higher densities through efficient exploitation of available resources. The strength of the relationship between range size and abundance is weak, however, and there exists considerable interspecific variation. The generality of this pattern needs to be verified through comparison with other tropical forest communities, analysis at different scales, and with corrections for phylogeny (Gaston 1990, Harvey and Pagel 1991).

4.5.3 Species turnover

A spectrum of opinion exists on the factors influencing the composition or assembly of species communities at particular sites and their variation over space and time. At one extreme, equilibrial models suggest that local communities are integrated, repeatable units whose composition is strictly regulated and predictable as a result of deterministic factors such as the varying environmental tolerances of species and competition (Clements 1916, MacArthur 1972, Diamond 1975a, Simberloff and Dayan 1991, Pandolfi 1996, Terborgh *et al*. 1996, Ganzhorn 1997, Pandolfi and Jackson 2001). In contrast, non-equilibrium approaches note that community composition varies substantially over space and time, apparently due to stochastic or historical effects of colonization and extinction (Gleason 1917, 1926, Whittaker 1970, Connor and Simberloff 1979, Strong *et al*. 1984, Hubbell and Foster 1986, Gascon 1991, Jenkins and Buikema 1998, Terborgh and Andresen 1998, Brown *et al*. 2001). A fundamental distinction between non-equilibrium and equilibrium models is that under the former, community composition may be expected to 'drift' or vary continuously through space and time, whereas the latter predicts that spatially or temporally independent sites with similar environmental conditions would have similar communities (Hubbell and Foster 1986, Terborgh *et al*. 1996). Using a space-for-time substitution approach, biological influences and deterministic structure have been demonstrated for communities of tropical rainforest trees (Terborgh *et al*. 1996, but see Terborgh and Andresen 1998) and birds (Terborgh and Weske 1975, Raman *et al*. 1998).

The composition of the rainforest bird community in the southern Western Ghats is shown here to be correlated with and influence significantly by elevation and tree species composition of sites. Geographic distance between sites, correcting for elevation, was not correlated to change in community composition as would be expected under a simple non-equilibrium model of effectively random species distributions and abundances with spatial autocorrelation (Terborgh *et al*. 1996). This was clearly exemplified by the high-altitude sites in Sengaltheri clustering with high-altitude sites far away (Neterikal trail, Kakachi,, and Kodayar) than to virtually adjacent sites that were at lower elevations. Temperature, irradiance, and other biological factors not measured in this study are known to correlate with elevation in tropical rainforests (Richards 1996). The elevation-specific environment and tree species composition thus appear to be of primary importance in determining bird community composition in the southern Western Ghats rainforests.

In addition, the pattern of species turnover with elevation indicated the occurrence of distinctive community composition at low-elevations (< 900 m) and high elevations (> 1,100 m), separated by a transitional zone of high turnover. This paralleled the observed range size distributions and placements of rainforest birds in KMTR. If confirmed through additional data on birds and habitat, the transition zones, in contrast to lower or higher elevations, may essentially be areas where communities are in flux due to relatively unpredictable or higher spatial and temporal variation in the rainforest environment for birds. Multi-year data would help test the prediction that inter-annual similarity in community composition would be lower in the transition zone as opposed to higher and lower altitudes. The occurrence of the transition zone at around 1,000-1,200 m elevation may be due to environmental changes related to the fact that this is the elevation at which regular cloud- and mist-cover begins to form during the monsoon months in the southern Western Ghats (M. B. Krishna personal communication) as in other tropical montane rainforest regions (Richards 1996).

4.5.4 Null models of community assembly

In large-scale community studies, where field experiments on community assembly and compositional changes are virtually impossible, null models evaluated using computer simulations offer the only method for critical evaluation of the role of chance factors and biological effects (Wiens 1989). Models with few or no constraints, which attempt to capture the effects of pure chance, almost invariably fail to explain community structure (Farnsworth and Ellison 1996, Terborgh *et al*. 1996). This may be due to the so-called 'Jack Horner' effect, with model failure illustrating only what is obvious (such as the differences in species richness or frequencies across sites in the real world, Wilson 1995). Such models must nevertheless be evaluated as possibly the most parsimonious explanation for observed patterns. Assessing models that incorporate a degree of biological realism has, however, greater potential to offer insights into community organization (Stone *et al*. 1996, Farnsworth and Ellison 1996).

In this study, I evaluated a hierarchy of models incorporating effects of chance and various explicit biological constraints (see Methods 4.3.3.5: Statistical analyses and null models). The results clearly indicate that non-equilibrium models, that do not incorporate essential biological constraints, fail to predict or reproduce the observed pattern of similarities in species composition between sites. The local community composition is thus jointly determined by limits on the number of co-occurring species and the elevational range sizes of species in the community. Furthermore, the non-random spatial distribution of birds, particularly the contiguous distributions of species along the altitudinal gradient must be factored in. Even with these constraints, the results indicate that assuming that species are distributed independently of each other can result in community similarities close to, but departing significantly from, those actually observed. Thus, Whittaker's (1970) models of local community structure as a consequence of overlapping species distributions along ecological gradients,

is only partly supported. The data suggests the possibility that some species have significantly higher overlap or avoidance due to biological determinants such as joint distributions up to ecotones or exclusive distributions due to competitive interactions (Terborgh 1971, 1985a). Such interactions need to be examined through field research on competition (e.g. Robinson and Terborgh 1995) as well as specific null models that simulate these dynamics (e.g. Dale 1986, 1988, Hofer *et al*. 1999, 2000); this is beyond the scope of the present analysis.

4.6 SUMMARY

Studies of species distributions on elevational gradients are essential to understand principles of community organisation as well as to conserve species in montane regions. This study examined the patterns of species richness, abundance, composition, range sizes, and distribution of rainforest birds along an elevational gradient in the Kalakad-Mundanthurai Tiger Reserve (KMTR). Fourteen sites spanning an elevational range of 500 to 1,400 m were sampled for birds using fixed-radius point counts and for habitat by standard methods. Past theory and empirical studies have suggested that as elevation increases species richness may decline or peak at mid-elevations. In contrast, this study found that resident bird species richness did not change significantly with elevation although the species composition changed substantially with less than 10% similarity (Morisita index) between the lowest and highest elevation sites. Different diet guilds showed varying elevational patterns. More frugivores and omnivores occurred at lower elevations, whereas insectivores and nectarivores dominated at higher elevations. Constancy in species richness was possibly due to relative constancy in productivity and lack of elevational trends in vegetation structure, while turnover was related to changing abiotic and biotic factors (elevation, tree species composition) along the gradient. Elevational range size of birds, expected to increase with elevation according to Rapoport's rule, was found to show a contrasting inverse U-shaped pattern because species with narrow elevational distributions, including endemics, occurred at both ends of the gradient (below 800 m and above 1,200 m). Bird species composition also did not vary randomly along the gradient as assessed using a hierarchy of null models of community assembly, from completely unconstrained models to ones with species richness and range-size distribution restrictions. Instead, bird community composition was correlated with elevation and tree species composition of sites. This asserts the significant influence of deterministic factors on bird community structure, although the effects of factors such as interspecific competition still needs to be explored. The results highlight the importance of rainforest areas at both low (< 800 m) and high (> 1,200 m) elevations for conserving rainforest bird diversity, particularly endemics. In addition, the tree species composition of sites is of particular importance in determining bird community composition. Conservation of low- and high-elevation areas and maintenance of tree species composition against habitat alteration are therefore important for bird conservation in the southern Western Ghats rainforests.

CHAPTER 5

Responses of tropical rainforest birds to abandoned plantations, edges, and logged forest in the Western Ghats, India

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CHAPTER 5

Responses of tropical rainforest birds to abandoned plantations, edges, and logged forest in the Western Ghats, India

5.1 INTRODUCTION

Secondary forests are now ubiquitous in tropical landscapes. This is particularly evident in regions of tropical rainforest, valued by conservationists for their remarkable species richness. In south Asia, as in the Neotropics, central Africa, and southeast Asia, tropical rainforests have been logged for timber, cleared and cultivated for agriculture, exploited for various natural products, submerged under reservoirs, and converted to plantations and other land uses. Such transformation of natural landscapes by human action has created over 400 million hectares of secondary forest (31% of total forest land) in tropical closed forest formations (Brown and Lugo 1990). As secondary forests increase in area in the tropics, there is a clear need to assess their conservation values through studies of their vegetation and animal communities (Brown and Lugo 1990, Richards 1996, Johns 1997).

Bird communities have been frequently used for conservation assessment and monitoring (Furness and Greenwood 1993). Past studies from tropical rainforest regions have shown that agroforestry plantations, logged forests, and secondary successional forests generally harbour fewer bird species and have altered community composition as compared to primary forest (Daniels *et al.* 1990a, Johns 1992, Thiollay 1995, Raman *et al.* 1998). The relationship between degree of habitat alteration and change in bird communities is, however, not precisely understood. The observed effects may be a non-linear function of disturbance intensity (Johns 1992) with the degree of change in bird community structure and composition in secondary forests being strongly related to the magnitude of alteration of rainforest vegetation structure and floristic composition (Raman *et al.* 1998).

Within the community, individual bird species differ in their responses and susceptibility to habitat alteration. Habitat changes have been reported to particularly affect rare and restricted-range birds, rainforest habitat specialists, and altitudinal migrants (Raman 2001). Other factors that influence susceptibility include body size, fecundity, diet-guild, and foraging strata (Terborgh and Winter 1980, Brash 1987, Kattan *et al.* 1994, Thiollay 1995, Sieving and Karr 1997, Castelletta *et al.* 2000), and abundance or rarity in undisturbed habitat (Diamond *et al.* 1987, Soulé *et al.* 1988, Caughley 1994, Warburton 1997, but see Marsden 1997). The generality of these patterns can be assessed by studies of various forms of habitat alteration in different tropical forest regions.

Within peninsular India, tropical evergreen rainforests are distributed along the Western Ghats mountain range in southwest India (Champion and Seth 1968). This region is one among the world's biodiversity hotspots, 200 most important ecoregions, and endemic bird areas (Olson and Dinerstein 1998, Stattersfield *et al.* 1998, Myers *et al.* 2000). Over the last century, in particular, the Western Ghats has seen significant transformation of its landscapes by human impact. Exploitation of forests for timber and land conversion for plantations such as teak, tea, coffee, cardamom, pepper, and *Eucalyptus* during the British colonial period continued after independence in 1947. Besides creating new, man-altered habitats in the landscape, much secondary forest areas were also created due to logging as well as abandonment of plantations (Chandran 1997). Chronic, low-intensity extractive use of forests also continues along the Western Ghats with significant effects on the tropical rainforest vegetation (Daniels *et al.* 1995).

This study focussed on the responses of tropical rainforest birds to disturbed forest habitats by documenting changes in bird abundance and community structure. Sites representing cardamom (*Eletteria cardamomum*) plantations abandoned for 5 and 15 years, plantation-rainforest edges, and a selectively logged patch were compared with adjacent primary tropical evergreen rainforest in the Kalakad-Mundanthurai Tiger Reserve in southern India. The main questions of the study were: (1) What are the changes in vegetation and bird community structure in disturbed forest sites? (2) Does bird community structure vary predictably with degree of alteration of forest vegetation structure and tree species composition? (3) What are the species correlates of susceptibility to habitat alteration? The results are compared with earlier findings from other tropical rainforest bird communities. I discuss the conservation values of abandoned plantations and logged sites and assess the need for habitat management and rainforest restoration for bird conservation.

5.2 STUDY SITES

5.2.1 Study area

The study was carried out in the Kalakad-Mundanthurai Tiger Reserve (KMTR, Chapter 2). The intensive study sites were located at Sengaltheri (8°31' N and 77°26' E) and Kakachi (8°33' N and 77°24' E). These areas contain rainforests ranging in altitude between 800 m and 1,400 m, which are

contiguous with rainforests elsewhere in the Reserve. The terrain is rugged, mountainous, and drained by many perennial streams. All bird sampling reported in this paper was restricted to between 1,040 m and 1,300 m asl.

5.2.2 Study strata and selected sampling sites

The following strata and sites were selected for study:

1) *Cardamom plantation abandoned for 5 years.*—Three sites (P1, P2, and P3) were selected in this stratum (henceforth referred to as 5-year abandoned plantation) at Sengaltheri, where the plantations were abandoned upon expiry of lease in 1995. P1 and P2 were less than 200 m apart, although P3 was about a kilometre away. When the plantation was established, most understorey trees had been cleared, although large native trees were retained and a few exotic trees (*Erythrina indica*) were planted as canopy shade trees. During the study, the shrub and sapling layer was virtually absent and still dominated by surviving cardamom clumps, and also contained weeds, ferns, grasses, and herbaceous plants (Plate 2). The three sampled sites were contiguous and surrounded by relatively undisturbed primary rainforest.

2) *Cardamom plantation abandoned for 15 years.*—A single site (P7, henceforth referred to as 15-year abandoned plantation), abandoned around 1983, was sampled in Kakachi. Superficially, this site resembled the 5-year abandoned plantation but the tree canopy appeared much sparser. Pioneer (*Macaranga indica, Debregesia longifolia*) and rainforest trees were growing in the understorey. The ground layer was still dominated by surviving cardamom plants, weeds, ferns, grasses, and herbs.

3) *Plantation-rainforest edges*.—Two sites (P4, P5) at the edges of the 5-year abandoned plantations in Sengaltheri and one (P6) between an abandoned *Eucalyptus* plantation and secondary rainforest vegetation in Kakachi were sampled. These sites appeared intermediate in structural and floristic alteration as compared to the abandoned cardamom plantations and were chosen to see if they were intermediate in bird community attributes. A key difference was the occurrence of woody shrubs in the understorey in this stratum.

4) *Logged forest.*—One site (T7) representing a selectively logged (probably at low intensity) patch of forest was sampled in Kakachi, near Kodayar. This site had few large trees, and a sparse canopy, with the pioneer tree *Macaranga indica* being quite common, as was bamboo in the understorey. The site was otherwise similar in many respects to primary rainforest. The logging was probably carried out when the nearby Kodayar reservoir was being constructed (1968–1978). Since then, the site has been abandoned and undisturbed except for limited fuelwood and timber removal by local people.

5) *Primary rainforest*.—Six undisturbed rainforest sites were sampled (T3, T4, T5, in Sengaltheri and T8, T9, T10 in Kakachi, see Plate 2). These had tree and liana (> 20 cm girth at breast height—1.3 m) densities of over 900/ha, with a maximum canopy height of about 30 m. The sites had a dense undergrowth of shrubs, herbs, and canes (*Calamus* spp.). The common canopy trees were *Cullenia exarillata, Palaquium ellipticum, Mangifera indica, Syzigium spp., Holigarna nigra, Aglaia eleagnoidea,* and *Cryptocaria bourdilloni*. Understorey trees included *Antidesma menasu, Agrostistachys borneensis, Epiprinus mallotiformis, Drypetes sp., Acronychia pedunculata, Eugenia sp.*, and *Nothopegia racemosa*.

5.3 METHODS

5.3.1 Vegetation sampling

Tree, shrub, and cane densities were measured and presence-absence of bamboo recorded as described in Chapter 4. Altitude, canopy cover and height, vertical stratification, and leaf litter depth were measured at 25 points as described in Chapter 4. A canopy overlap index was given following the method of Daniels *et al.* (1992). A rank of 0 was given when there was none overhead, 1 when the branches of adjacent trees did not overlap above, 2 when the branches overlapped but the sky could be seen through the leaves, and 3 when there was complete overlap and the sky was not visible overhead.

5.3.2 Bird surveys

The fixed-radius point count method was used to survey bird populations at each site. The details of the sampling method are described in Chapters 3 and 4. At each site, 25 point count surveys (yielding 122–245 detections and an estimated 265–577 individual birds per site) were carried out, excluding the logged forest patch in which only 18 point counts were sampled because of logistical difficulties. Sampling was carried out mostly between February and May 1998 (the 15-year plantation was sampled in March 1999), when resident and migrant birds were present in the plots. Some sampling was also carried out on bright, sunny days between June and August 1998. As migrant birds were not present when this sampling was carried out, resident birds are considered separately in the analyses.

5.3.3 Analyses

The six primary rainforest sites were those also described in Chapter 4, the other sites mentioned here were sampled additionally. Vegetation variables were analysed as described in detail earlier (Chapter 4). The vegetation variables were summarised using principal components analysis in order to identify sets of inter-correlated variables as components, with each component not correlated to the others. The components representing the vegetation gradient could then be related to bird responses (Pielou 1984). The analysis was performed on the correlation matrix of the variables (for standardisation)

using SPSS software and the resulting factor matrix was rotated by the Equamax method. This rotation simultaneously minimizes the number of variables loading highly on a factor and the number of factors needed to explain a variable, enabling easier interpretation. Principal component factor scores were calculated from the factor score coefficients and normalised z-scores of the variables.

Bird species richness (cumulative species recorded, species per point count, and Coleman rarefaction estimates), bird species diversity (Shannon-Weiner index), and bird abundance were derived as explained in Chapter 4, standardised for 17 point counts. Since the replicate points sampled within a site may not have been strictly indpendent due to proximity effects, differences between sites in bird species richness, number of detections, and bird abundance were tested using repeated-measures analysis of variance (Sokal and Rohlf 1981). Similarity in bird community and tree species composition between sites was computed using the Morisita index and correlations between similarity/distance matrices were assessed using Mantel tests as described earlier (Chapter 4). Relationships between bird community and vegetation components (PCs) were assessed using Kendall correlations (Siegel and Castellan 1988).

Bird responses to the different habitat changes (study strata i to iv) were assessed using a simple persistence index (PI, modified from the response index of Davies *et al.* 2000). The persistence index was defined as the ratio of the average density of the species in the stratum to its average density in rainforest. The PI can be considered as an index of population decline or increase as species that declined in the stratum relative to rainforest had PI<1, while those that increased had PI>1. PI values were calculated for all species in each stratum (5-year and 15-year abandoned plantations, edges, and logged). Species were classified into eight diet-guilds and three broad foraging strata categories (terrestrial, understorey, and canopy) using natural-history information from Ali and Ripley (1983) and personal observations. The body mass of each species was obtained from averages (or mid-points if only range was available) given by Ali and Ripley (1983). In a few cases (eg. Oriental Dwarf Kingfisher) where data were unavailable, body mass was approximated using values available for similar species. In order to see if persistence was related to rarity and body mass, Kendall partial rank-order correlation coefficients were calculated (Siegel and Castellan 1988). Difference in PI values of species belonging to different diet-guild and foraging strata categories were tested using non-parametric Kruskal-Wallis analysis of variance (Siegel and Castellan 1988).

5.4 RESULTS

5.4.1 Vegetation changes across strata

There were noticeable differences in vegetation across strata. The most obvious and visible changes were in foliage profile. The percentage of points with foliage in the eight height intervals was significantly different across the five strata ($\chi^2 = 75.63$, $df = 28$, $P < 0.001$; Figure 5.1).

In comparison with primary rainforest, the 5-year abandoned cardamom plantation had substantially lower percentage of points with foliage in the height intervals between 2 and 16 m. This reflected the relative paucity of shrubs and understorey trees. The 5-year plantations, however, had a greater proportion of points with foliage above 24 m compared to rainforest, indicating the well-developed canopy of large, remnant shade trees in the plantation. Interestingly, the 15-year abandoned cardamom plantation had greater percentage of points with foliage than the 5-year plantation in the height intervals between 2 and 8 m, indicating the contribution of regenerating shrubs and pioneer trees in these vertical strata. The 15-year plantation had substantially less foliage than primary rainforest between 8 and 16 m, again indicating absence of understorey trees.

In contrast to the abandoned cardamom plantations, the logged patch showed similar foliage profile at heights below 16 m when compared with primary rainforest. The logged patch had, however, substantially fewer percentage of points with foliage in the height intervals between 16 and 32 m, indicating the effects of removal of large trees on the foliage distribution. The plantation-rainforest edges showed a foliage profile similar to primary rainforest, but with lower percentage of points with foliage in all height classes (Figure 5.1).

There were notable differences in other vegetation attributes. Average canopy cover was above 92% (92.9 – 95.8%) in all the primary rainforest sites. In the other strata, average canopy cover was lower, being 90.6 – 91.4% in 5-year plantation, 72.1% in the 15-year plantation, 79.3 – 91.2% in edges, and 90.4% in the logged site. The primary rainforest sites also had higher vertical stratification, litter depth, and basal area, and lower horizontal heterogeneity as compared to three sites (*Eucalyptus*-rainforest edge, 15-year abandoned plantation, and logged sites), while the other sites had intermediate values. Tree and shrub densities were also higher in primary rainforest, lower in 5-year and 15-year plantations, and intermediate in the edges. Notably, the logged site and *Eucalyptus* edge had high tree and shrub densities, although the basal area was low.

Cane was present at high densities (average of 2.4 – 25.2 plants/plot) in the primary forest and logged sites, but absent in the abandoned cardamom plantations, and occurring at intermediate abundance in the edges (0.6 – 2.4 plants/plot). A converse pattern was found in the distribution of cardamom. Cardamom was absent in primary rainforest (except for one clump recorded in T3), logged site, and *Eucalyptus* edge. Cardamom densties were high in the 5-year (average of 2.5 – 3.5 clumps/plot) and 15-year plantations (2.9 clumps/plot) and intermediate in two edge sites (P4 and P5, 0.4 – 1.3 clumps/plot). Bamboo occurred patchily in the logged site, primary rainforest sites, and edges, and, like cane, was absent from the abandoned plantations. For the standardised sample of 52 trees, tree species richness was lowest in *Eucalyptus* edge (14 species), intermediate in the abandoned cardamom plantations and logged site (20 – 21 species), and highest in primary rainforest and the other two edge sites (23 – 31 species, except T9 that had 13 species).

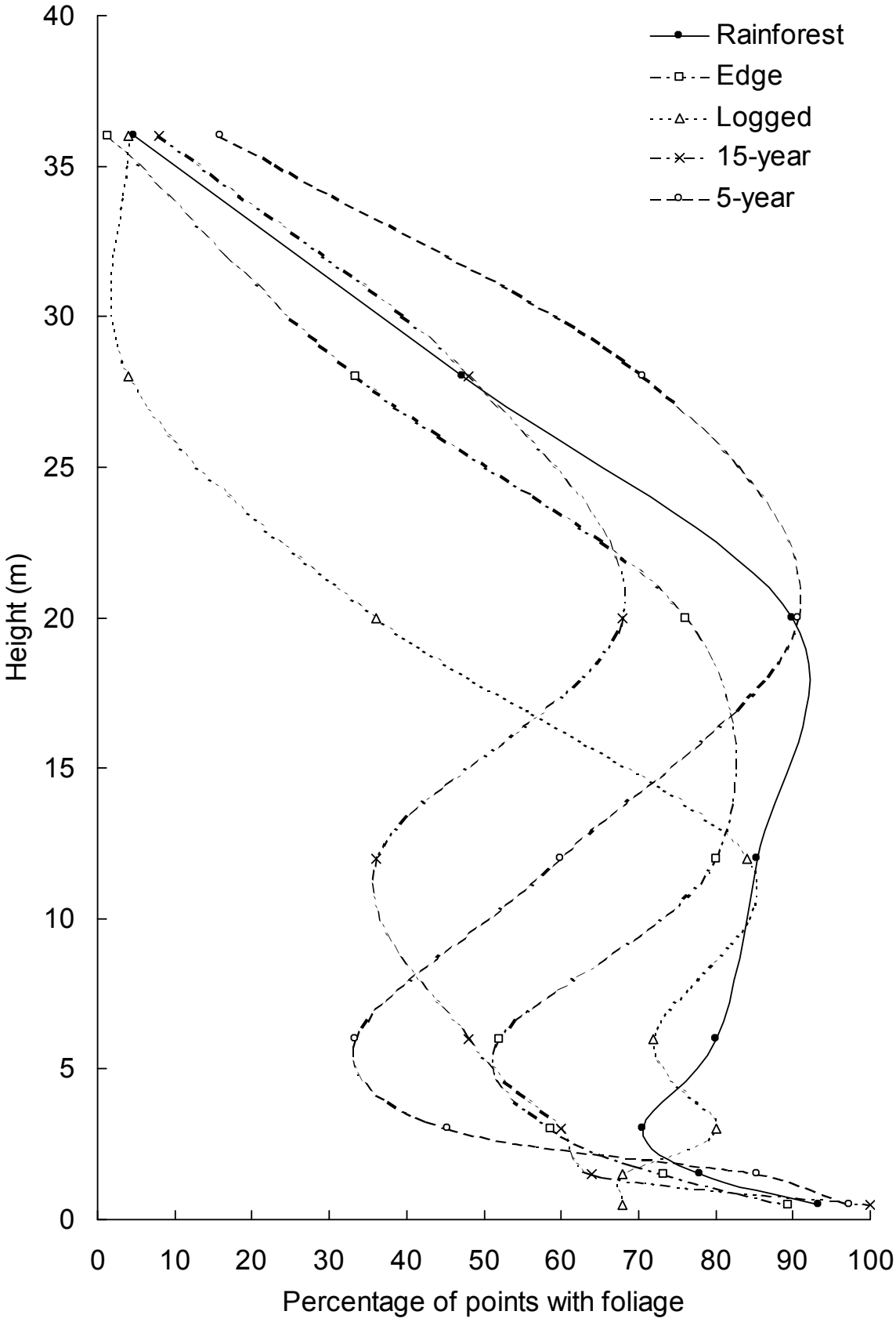

Figure 5.1: Foliage profile in the different disturbed rainforest strata and primary rainforest in the Kalakad-Mundanthurai Tiger Reserve. For strata with replicate sites, percentage of points with foliage in each height interval was averaged across sites. Smoothed curves are used to join percentage values plotted against mid-points of the height intervals sampled.

5.4.2 Cluster analysis and ordination using vegetation parameters

To examine similarities between sites in their vegetation structure, principal components analysis and ordination were used. Principal components analysis extracted three components representing 81.9% of the total variation in the data set (Table 1). The first component (PC1), explaining 34.6% of the variation, was strongly positively related to tree, shrub, and cane densities, weakly to canopy rank, and negatively to litter depth and density of cardamom clumps. PC1 can thus be taken to indicate woody plant densities. PC2, explaining 34.2% of the variation, was related to forest structural attributes; it was positively correlated with canopy variables, vertical stratification, and basal area, and negatively with horizontal heterogeneity. PC3 (13.1% of the variation) was positively related only to tree species richness.

The major changes along the vegetation gradient are clearly encapsulated when the sites are plotted in the ordination diagram using their PC1 and PC2 scores (Figure 5.2). The primary rainforest sites have relatively high PC1 values, reflecting high woody plant densities, and high PC2 values, indicating well-developed forest structural attributes and low horizontal patchiness. The logged and *Eucalyptus* edge site, have high PC1 scores due to relatively high woody plant density, but low PC2 scores because of low basal area, canopy cover, and vertical stratification. Two primary rainforest sites (T3 and T5) had low PC1 values similar to the edge sites. The abandoned cardamom plantations are at the lower end of the gradient on PC1 due to very low woody plant densities and an understorey still dominated by cardamom clumps. Two edge sites (P4 and P5) were intermediate between plantations and rainforest. Within the abandoned cardamom plantations, the 15-year plantation site was lower on the PC2 axis than the 5-year sites indicating sparser canopy, lower vertical stratification, and higher horizontal patchiness (Figure 5.2).

Table 5.1: Results of principal components analysis of forest vegetation variables in disturbed and undisturbed rainforest sites in the Kalakad-Mundanthurai Tiger Reserve.

	Principal components		
	PC1	PC2	PC3
Eigen value	4.2	4.1	1.6
Variance explained (%)	34.6	34.2	13.1
Cumulative variance (%)	**34.6**	**68.8**	**81.9**
Factor matrix[a]			
Tree (> 30 cm girth at breast height) density	**0.907**	0.002	-0.007
Shrub density	**0.933**	0.178	-0.001
Cane density	**0.750**	0.301	-0.320
Density of cardamom clumps	**-0.870**	0.008	-0.306
Litter depth	**-0.604**	0.508	0.348
Canopy rank	**0.595**	**0.578**	0.413
Canopy height	-0.283	**0.929**	-0.002
Canopy cover	0.391	**0.597**	0.524
Vertical stratification	0.272	**0.917**	0.161
Horizontal heterogeneity	-0.311	**-0.784**	-0.156
Basal area of trees > 30 cm GBH	-0.002	**0.839**	0.005
Tree species richness	-0.139	0.002	**0.866**

[a] Pearson's correlations with original variables (df = 12); significant ones ($P < 0.05$) are in bold.

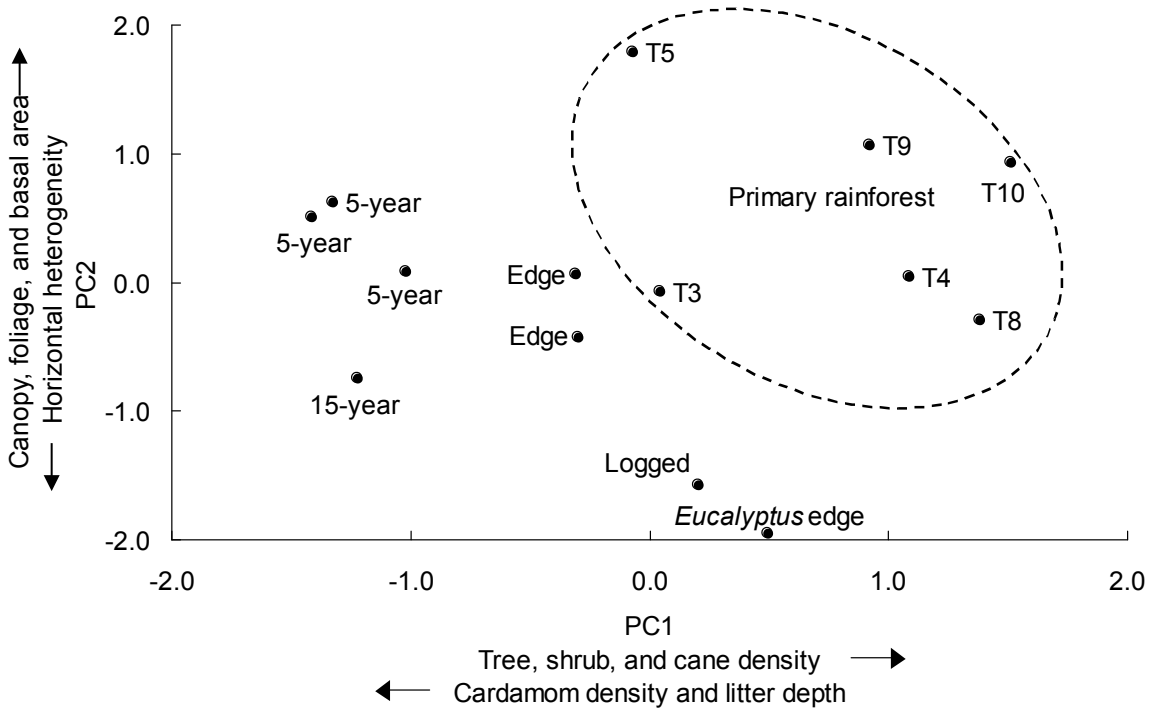

Figure 5.2: Ordination of sampled sites using the principal component scores PC1 and PC2. The ellipse is drawn by eye to indicate primary rainforest sites.

5.4.3 Trends in bird species richness and abundance

A total of 2433 detections comprising an estimated 6047 individual birds belonging to 52 species was obtained during the study (Appendix). Seven (13.5%) bird species were not seen in any of the abandoned plantations and rainforest edges. These were Grey-breasted Laughingthrush (endemic to Western Ghats), Rufous Woodpecker, White-bellied Woodpecker, Oriental Dwarf Kingfisher, Crested Serpent Eagle, and Eurasian Blackbird. All these species were relatively rare in primary rainforests. Species seen only in the disturbed habitats and absent in primary rainforests were the Red-whiskered Bulbul (resident), and Blyth's Reed Warbler and Pied Thrush (migrants). Two other resident species detected occasionally in point count surveys in disturbed habitats but not in primary rainforests were the Hill Myna and White-bellied Treepie. These two species were, however, seen frequently in rainforests during opportunistic observations.

Comparison of bird species richness using rarefaction showed discernible, although relatively moderate, differences between strata (Figure 5.3). Bird species richness was lowest in 5-year abandoned cardamom plantations and highest in the primary rainforest and logged sites. The 15-year abandoned cardamom plantation and rainforest-plantation edges had intermediate values (Figure 5.3). The number of bird species, detections, and individuals per point showed a similar pattern, with the 5-year plantation having lowest and logged and primary rainforests having highest values (Figure 5.4). Repeated-measures analysis of variance indicated significant effects of stratum on these three variables ($F > 4.13$, $df = 4$, $P < 0.05$). The within-subject or repeated-measures (points) effect was not

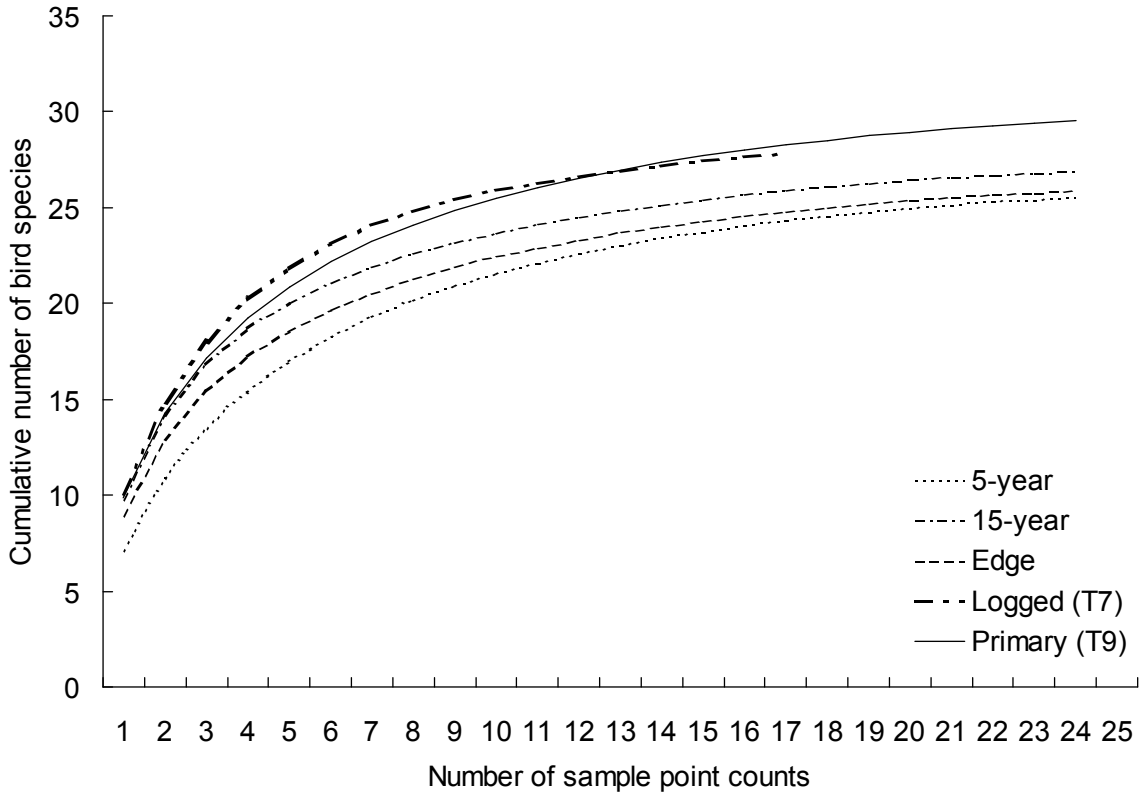

Figure 5.3: Rarefaction curves of bird species richness with sampling effort in the different strata in the Kalakad-Mundanthurai Tiger Reserve. For strata with replicate sites, estimated species richness curves were averaged across sites.

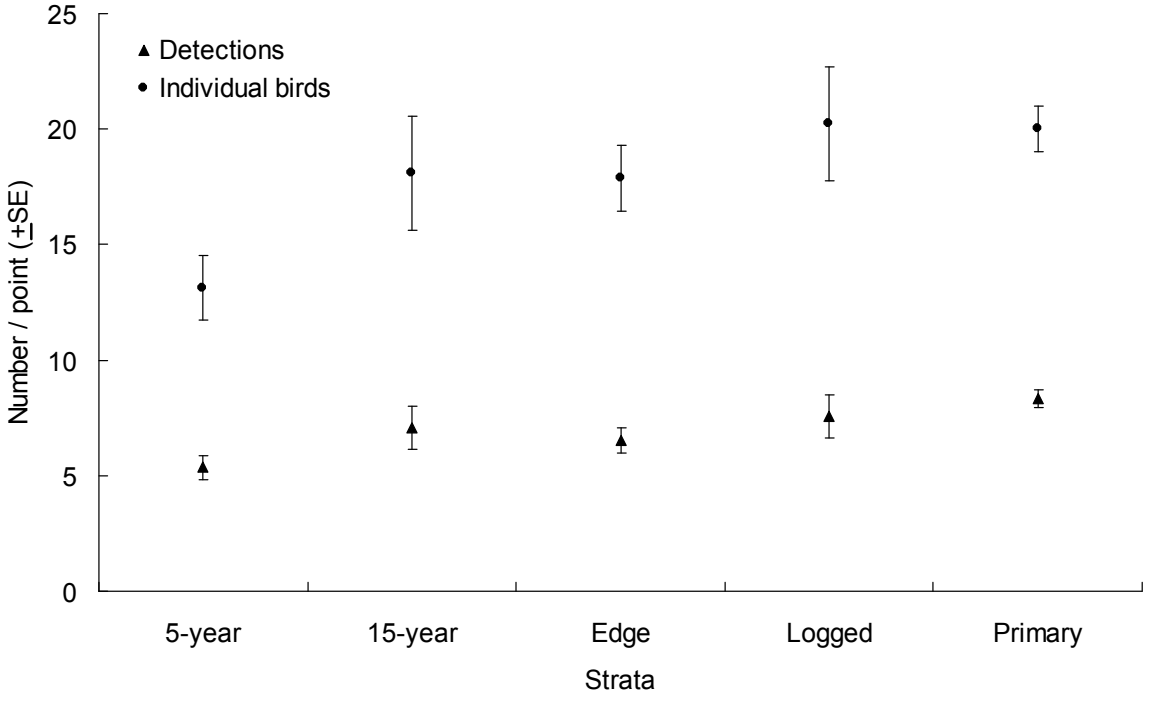

Figure 5.4: Variation in bird detections, and abundance in point count censuses in the different strata in the Kalakad-Mundanthurai Tiger Reserve.

significant ($F < 1.24$, $df = 17$, $P > 0.24$). There was also no significant interaction effect between point and stratum ($F < 0.99$, $df = 68$, $P > 0.51$).

5.4.4 Correlations between bird community and vegetation

To examine relationships between vegetation structure (represented by the principal component scores) and bird community attributes, non-parametric Kendall correlations were used. Bird species richness (rarefaction value after 17 point counts surveys) was correlated to the site scores representing woody plant density (PC1, Kendall $\tau = 0.582$, $df = 12$, $P = 0.004$). Indices of resident bird species richness (overall, number of resident species seen at least twice, and average resident species detected per point) were all significantly positively correlated to PC1 ($\tau > 0.540$, $P < 0.01$; Figure 5.5a). The correlation between bird species diversity and PC1 was positive but not highly significant ($\tau = 0.354$, $P = 0.079$). Bird abundance, measured as the number of individual birds per point, was also significantly positively correlated to PC1 ($\tau = 0.429$, $P = 0.033$). None of the bird community parameters were significantly correlated to PC2 or PC3 scores or the altitude of the sites.

The above bird community indices do not reflect changes in relative abundance of individual species as a consequence of habitat changes. Changes in bird community composition in the study sites were thus assessed by comparing all sites to one of the primary rainforest sites (T9) that was virtually undisturbed and had highest bird species richness. Similarities in bird community composition between each site and T9 (Morisita index) were computed and correlated with the PC scores. Again, similarity in bird community composition with primary forest was significantly positively correlated only to PC1 ($\tau = 0.606$, $df = 11$, $P < 0.01$). Thus, sites with higher scores of PC1 reflecting higher woody plant densities were more similar in bird community composition to primary rainforest (Figure 5.5b). Again, there were no significant correlations with PC2 and PC3.

5.4.5 Bird species turnover and similarity between sites

A dendrogram illustrating similarities in bird community composition between sites was produced using average linkage (between groups) cluster analysis (Figure 5.6). The input for the cluster analysis was a matrix of pair-wise similarities between sites (Morisita index) in bird community composition. The dendrogram shows four primary rainforest sites clustering together and being distinct from the other sites. Two primary rainforest sites (which had lower PC1 scores, see Figure 5.5b) were, however, linked to some of the disturbed habitats. In general, there was some tendency for sites within a stratum to be more similar to each other, apart from the edge sites and one 5-year plantation site (Figure 5.6).

Mantel tests were used to determine if bird species compositional similarity between sites was related to similarities in tree species composition and foliage profile, and elevational distance between

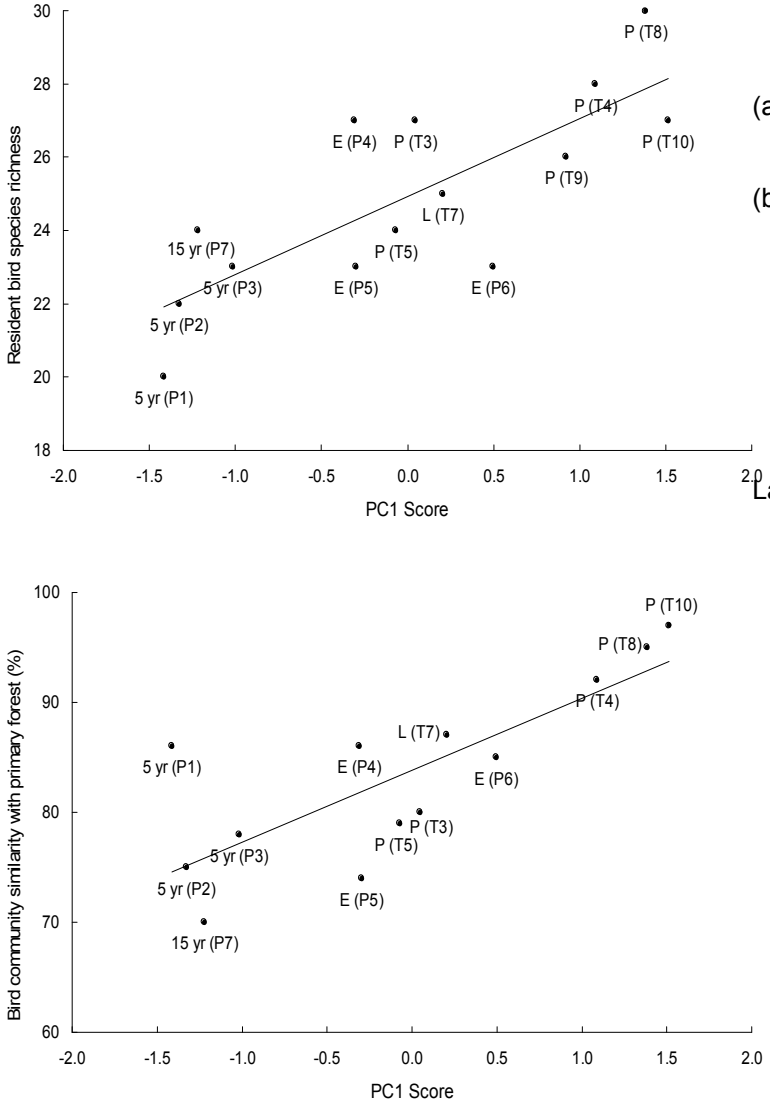

Figure 5.5: Relation between the vegetation component representing woody plant density (PC1) and
(a) resident bird species richness across sites (upper panel), and
(b) bird community similarity (Morisita index) of sampled sites with one reference primary forest site (lower panel) in the Kalakad-Mundanthurai Tiger Reserve.

Label legends:
5yr = 5-year abandoned plantations
15yr = 15-year abandoned plantations
E = edge sites
L = logged site
P = primay rainforest

sites. Similarity in bird community composition was significantly positively correlated with similarity in tree species composition (Mantel test, $K_r = 246$, $P = 0.0076$; Figure 5.7a), but not with similarity in foliage profile ($K_r = 22$, $P = 0.38$; Figure 5.7b). Elevational distance between sites was not significantly correlated to bird community similarity ($K_r = 111$, $P = 0.13$), tree species similarity ($K_r = 68$, $P = 0.23$), or foliage profile similarity ($K_r = 111$, $P = 0.12$) between sites.

Mantel tests between the independent variables revealed that only similarity in tree species composition and similarity in foliage profile were correlated ($K_r = 280$, $P = 0.0021$). Partial Mantel tests were used to examine the influence of each variable controlling for the other. Bird community composition was not correlated to similarity in foliage profile when tree species similarity was controlled for (partial Mantel test, $T = –0.045$, $P = 0.69$). Conversely, bird species composition was significantly correlated with similarity in tree species composition even after controlling for the effect of similarity in foliage profile ($T = –0.236$, $P = 0.0063$). This reinforces the earlier result indicating the influence of tree species composition on bird community composition.

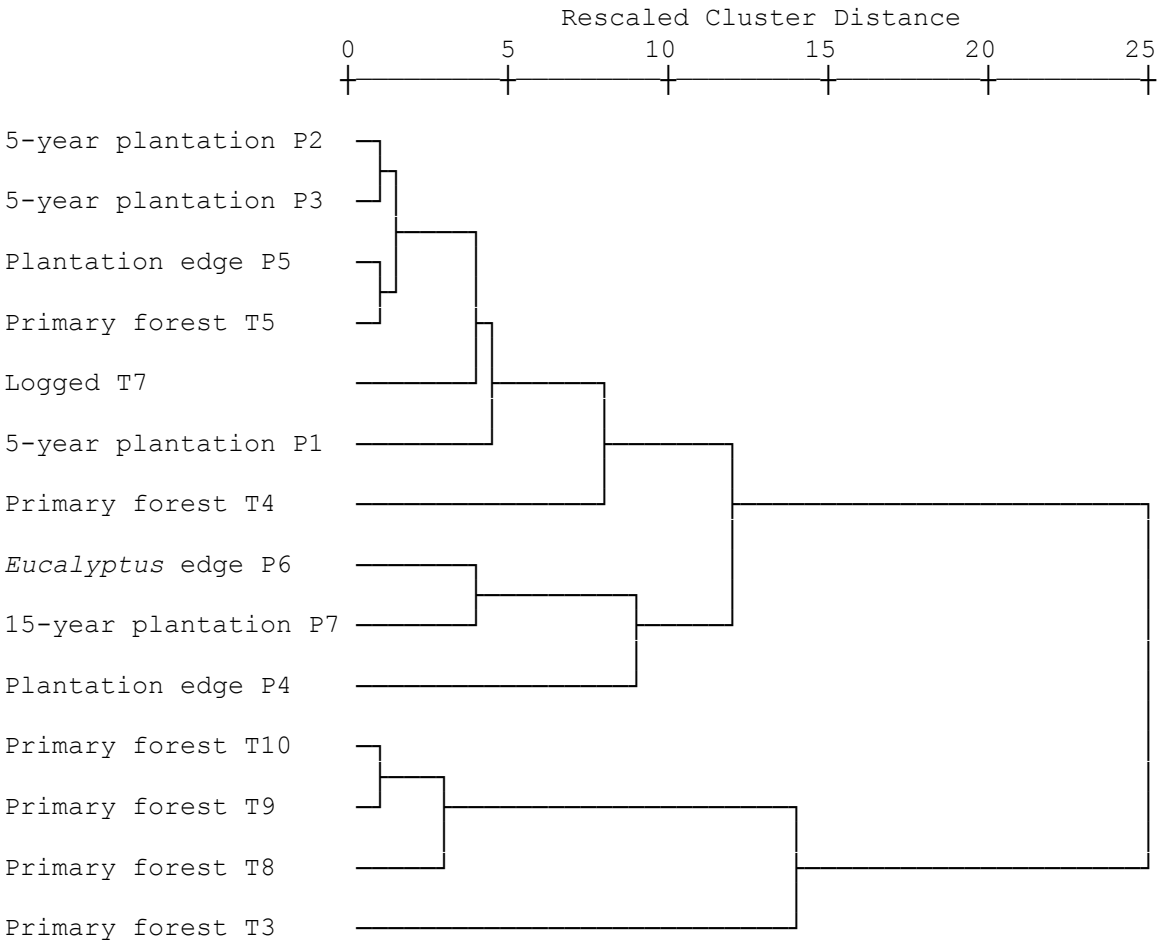

Figure 5.6: Cluster analysis dendrogram illustrating similarity between sites in bird community composition in the Kalakad-Mundanthurai Tiger Reserve.

5.4.6 Species attributes and persistence in disturbed habitats

Persistence index (PI) values were compared among different species categories to assess the influence of these species attributes on the susceptibility of birds to habitat changes. The results indicate that most species categories in most strata have average PI values less than 1 (Figure 5.8). This suggests that the different forms of habitat alteration result in generally lowering the abundance of bird species as compared to rainforest. There was, however, wide variation among species and some categories appeared relatively more sensitive.

Rarity and body mass.—The abundance of bird species in primary rainforest was negatively correlated to body mass (τ = –0.28, *df* = 45, *P* = 0.006). In each strata, avian persistence was significantly positively correlated with abundance when the effects of body mass were controlled for.

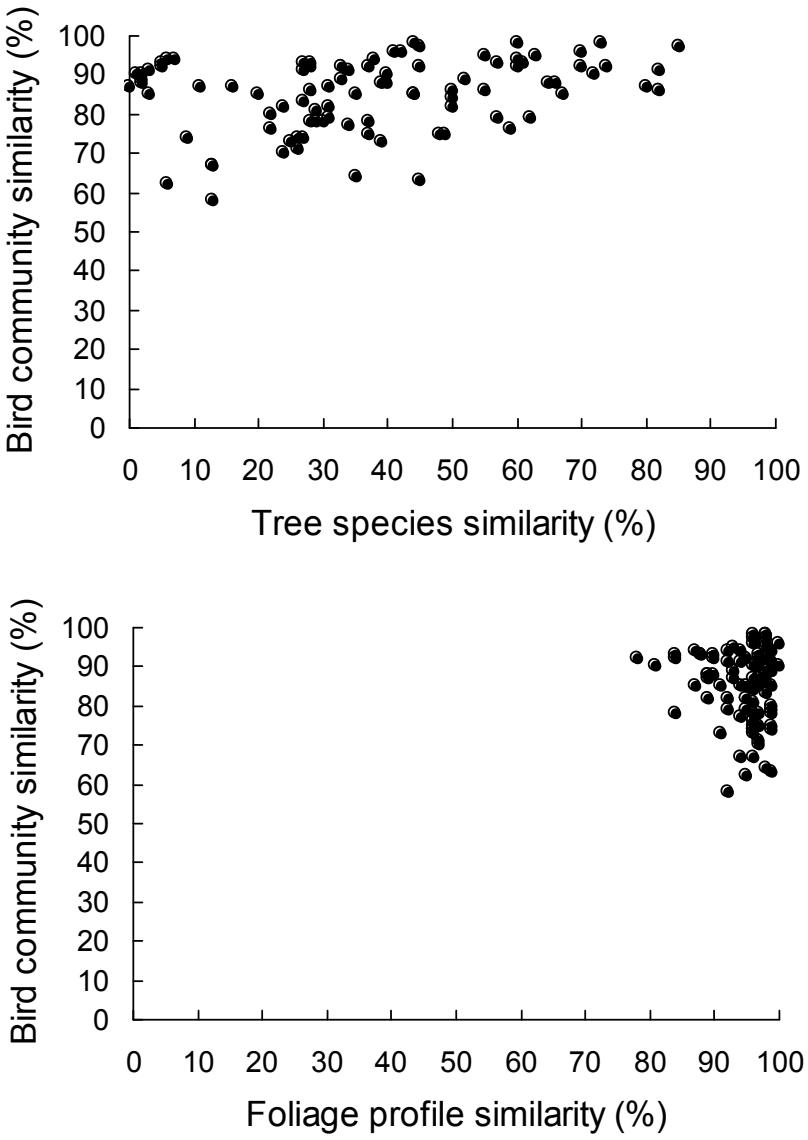

Figure 5.7: Pair-wise similarities between sites in bird community similarity in relation to similarities in (a) tree species composition (upper panel) and (b) foliage profile (lower panel) in KMTR.

The correlation was weaker in 5-year and 15-year abandoned plantations (Kendall partial rank-order correlations, $T = 0.17$ and 0.18, respectively, $df = 44$, $P < 0.05$) as compared to edge and logged sites ($T = 0.31$ and 0.40, respectively, $P < 0.01$). Body mass did not have a significant independent effect on persistence in 5-year abandoned plantations and edge sites ($T = –0.10$ and –0.01, respectively, $P > 0.05$), although it was significantly negatively related to persistence in 15-year plantations and logged sites ($T = –0.30$ and –0.25, respectively, $P < 0.01$). The results indicate the greater persistence of common species and a higher susceptibility of rare species to habitat disturbance.

Diet-guild.—Diet-guild also had an influence on PI values. These differences between diet-guilds in PI values were statistically significant in the 15-year abandoned plantations (Kruskal-Wallis ANOVA

by ranks, $H = 17.46$, $N = 47$, $P = 0.015$) and marginally significant ($H = 13.66$, $P = 0.058$) in logged forest (Figure 5.8a). The differences were not statistically significant in the 5-year plantations ($H = 9.08$, $P = 0.247$) and edge sites ($H = 8.52$, $P = 0.289$). Terrestrial insectivores and carnivores had low average PI values in all strata except in logged forest. Except in the 15-year plantation, bark-surface feeders had low PI values in other strata. Omnivores had relatively low average PI values in all strata (Figure 5.8a).

Foraging strata.—Terrestrial birds appeared to be related to low average PI values in all sites, whereas understorey birds had relatively low average PI values in 5-year and edge sites only. Canopy birds had relatively higher average PI values, particularly in 15-year plantations. The differences were statistically significant only in the 15-year plantations ($H = 6.49$, $P = 0.040$), and not in the 5-year plantations ($H = 3.20$, $P = 0.20$), edge ($H = 2.97$, $P = 0.227$), or logged sites ($H = 4.60$, $P = 0.10$, Figure 5.8b).

5.5 DISCUSSION

5.5.1 Effect of habitat alteration

Alteration of rainforest habitat had discernible effects on the bird community. These included reductions in bird species richness, abundance, and diversity, and changes in species composition, particularly in the abandoned cardamom plantations. Most species tended to occur at lower densities in the altered habitats, but few appeared to decrease substantially in abundance or disappear altogether. In contrast, few species appeared to increase in abundance in altered habitats and only three species were recorded solely from these habitats. Of these, two (Blyth's Reed Warbler and Red-whiskered Bulbul) are widespread common species occurring abundantly in disturbed second-growth and more open forest habitats, and the other (Pied Thrush) was detected only once during the study.

Several factors are possibly involved in the relatively moderate effects noticed in this study. A primary factor is the rainforest-dominated landscape of the study area. All the plantation and logged sites in the study area were adjacent to and continuous with primary rainforest or surrounded by it. The Agasthyamalai range of mountains, of which the study area forms a part, contains one of the last remaining large tracts of continuous rainforest (over 400 km²) in the Western Ghats (Ramesh *et al.* 1997, Johnsingh 2001). It is plausible that logged sites or plantations in a landscape dominated by disturbed and secondary habitats and containing only rainforest fragments will have more altered bird communities (Andren 1994). Also, the sites were relatively undisturbed after being abandoned (5-15 years for plantations and >30 years for the logged site) and did not suffer from chronic human impacts that can lead to further vegetation changes (Daniels *et al.* 1995). Another influential factor is that most rainforest birds in the Western Ghats appear to be generalist or adaptable species capable of thriving in a variety of habitats (Daniels 1989). The study also provides only a conservative assessment of the

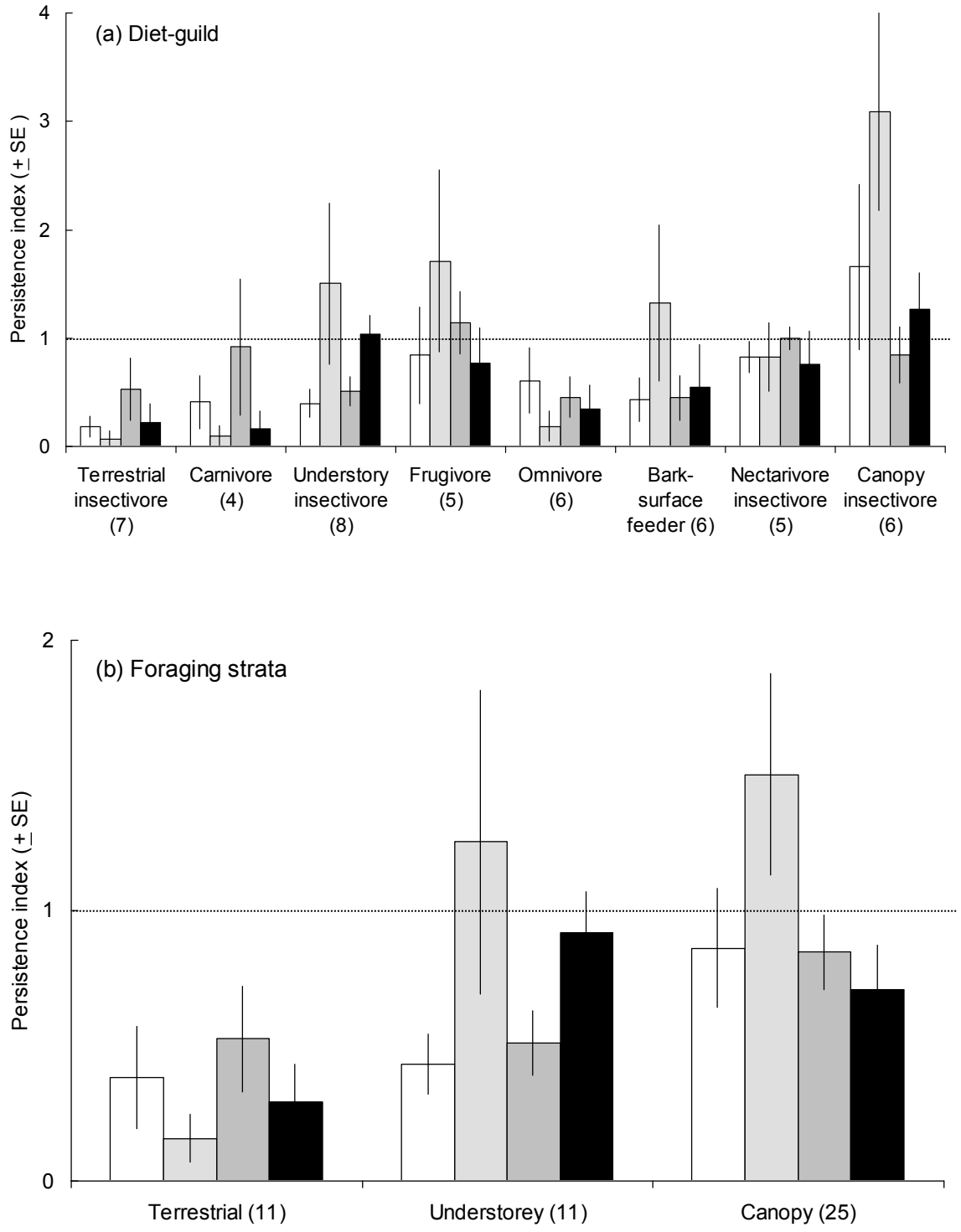

Figure 5.8: Persistence of rainforest bird species in relation to (a) diet-guild (upper panel) and (b) foraging strata (lower panel) in 5-year abandoned cardamom plantations (unshaded), 15-year abandoned cardamom plantations (stippled), edges (shaded grey), and logged (solid bar) sites in Kalakad-Mundanthurai Tiger Reserve. Figures in parantheses refer to number of species in each category.

impacts of habitat changes because of the use of a fixed-radius point count survey method. Better detectability of species in the relatively more open disturbed sites could have contributed to a bias against primary forest in estimates of abundance and species richness, although other analyses are unlikely to have been substantially affected by the slight bias.

5.5.2 Correlates of bird species persistence

Species also varied widely in their responses to habitat alteration. This variation, even within particular categories or guilds, suggests that species responses may be idiosyncratic. That responses may be dependent substantially on the unique natural history and ecology of individual species has been recognised earlier (Wiens 1989, Simberloff 1994). In addition, part of the variation may be due to chance and sampling effects, especially for infrequently detected species.

Some species attributes did, however, appear to be related to increased susceptibility to habitat alteration. Birds that were rare and those that were large-bodied tended to be more susceptible to habitat changes, a pattern consistent across the different forms of habitat disturbance studied here. The influence of both attributes, abundance and body size, is not surprising since these two variables are usually negatively correlated, with larger birds tending to be rarer (Carrascal and Telleria 1991, Silva *et al.* 1997). When the effects of body size were statistically controlled, abundance continued to have a consistent effect, although the reverse was true (controlling abundance) for only two strata. That rare birds are relatively more affected by habitat alteration is significant from a conservation perspective since it diminishes the value of disturbed habitats if they contain predominantly common and widespread species (Usher *et al.* 1986). A similar pattern of widespread, common species benefiting from habitat disturbances at the cost of rare and specialised species has been noted in other studies (Leck 1979, Raman 2001).

Birds that are rare in rainforest are so mostly because of their need for larger areas for ranging and specific resources or niches that are naturally scarce in the habitat (Thiollay 1994). Rare and large-bodied birds decline disproportionately in abudance in altered habitats possibly because of diminution of the available habitat area as well as available niche-resources. Besides rarity, other factors such as foraging strata and diet-guild also affected the persistence of species in disturbed habitats. Among diet-guilds, terrestrial insectivores appeared particularly susceptible to habitat alteration. The low PI values, especially in the abandoned cardamom plantations, can be attributed to the relatively sparse vegetation cover on the ground, largely because of the paucity of shrubs, saplings, and cane plants. Johns (1989) also noted declines in terrestrial and understorey insectivorous birds after logging in south-east Asia. It is not known, however, whether it is the paucity of vegetation (serving as cover from predators and nesting or foraging substrate) itself or indirect, negative effects on arthropod availability, or both, which leads to declines in insectivorous birds. Lowered tree density is likely to have had negative consequences for populations of bark-surface feeders such as

woodpeckers and nuthatches, as noted in a few other studies (Johns 1989, Thiollay 1995, Raman *et al.* 1998). As a consequence of their wider dietary flexibility, omnivores could be expected to do better in disturbed habitats than more specialised birds (May 1982). A contrary pattern was observed here. A possible explanation is that although omnivores may find some kinds of food in the disturbed habitats, the quantities available are lower than in primary rainforest. The persistence of carnivores appeared to be low in some habitats, although low sample sizes precludes firm conclusions or inference of possible causes.

Canopy-insectivores, frugivores, and nectarivores-insectivores showed relatively high persistence, in contrast to patterns observed in studies of other forms of habitat disturbance (Terborgh and Winter 1980, Bowman *et al.* 1990, Thiollay 1995, Raman *et al.* 1998). The frugivores and nectarivore-insectivores were all canopy birds and thus, as a class, canopy birds showed high persistence. This pattern is linked to the retention of native trees in the canopy in all the sites. Even within sites with low tree density (abandoned plantations), most of the large trees were retained for shade and basal areas remained high (Parthasarathy 2001). These large canopy trees contribute to most of the fruit crop (and possibly flower abundance) in the rainforest (T. R. S. Raman, unpublished data). Thus, unlike under disturbance regimes which lead to severe reductions of large trees and change in species composition, the frugivore, nectarivore-insectivore, and canopy insectivore guilds did not suffer major reductions in the present study.

5.5.3 Recovery of rainforest habitat

Overall, it is clear that the retention or maintenance of key attributes of the rainforest vegetation structure and composition is needed to maintain a relatively intact bird community structure and composition. A higher density of trees, shrubs, and cane plants, as reflected by PC1 in this study, appears to be particularly important in augmenting bird abundance and species richness and increasing the similarity of disturbed sites with primary rainforest. Past studies, including the classic work of MacArthur and MacArthur (1961), and others (Terborgh 1985b, Raman *et al.* 1998) have highlighted the positive effects of forest structure on bird species diversity. Forest structure as indexed by canopy measures, vertical stratification, and foliage profile did not appear to influence bird species richness, abundance, or community composition in this study. This is possibly because the range of variation in these attributes was less than that observed in other attributes such as tree species similarity (Figure 5.7). It is possible that alteration of forest structure may be tolerated by most bird species up to a threshold level and only more drastic changes (such as forest clearing and succession, Raman *et al.* 1998) will effect changes in bird communities.

In contrast to foliage profile, the present study suggests a greater influence of tree species composition on the bird community composition. The influence of floristic composition has been relatively neglected in bird community studies (Wiens 1989). While plant-dependent guilds such as

frugivores and nectarivores may depend directly on floristic composition, other guilds such as insectivores too may be affected by species-specific variation in foliage structure and foraging substrate (Robinson and Holmes 1984). The recovery of floristic composition may thus have a key role to play in the recovery of bird communities after habitat disturbances.

A noteworthy result is that despite being in a rainforest-dominated landscape, the abandoned plantations and logged sites do not appear to have recovered substantially over time even in the absence of major disturbances. A similar result was noted by Johns (1989, 1992) of incomplete recovery of rainforest bird community structure even 12 years after logging in Malaysian rainforests. In the present study, the bird species richness increased very slightly in abandoned cardamom plantations between 5 and 15 years. This was accompanied by some vegetation changes, such as establishment of some pioneer trees in the understorey, although the ground layer was still covered by surviving cardamom plants. Although some birds, such as understorey and canopy insectivores appeared to increase in abundance, bird community composition changed to the extent that the 15-year plantation was less similar to the adjacent undisturbed primary rainforest site (T9) than the more distant 5-year plantations were to T9 (Figure 5.5b). Although this result could be due to a greater level of initial disturbance or alteration in the 15-year site, the results do suggest that leaving the abandoned plantations for natural regeneration may not necessarily lead to recovery of typical rainforest communities, at least in the short term.

5.5.4 Conclusions

In a rainforest-dominated landscape, sites that have faced moderate habitat alteration continue to support a large complement of the rainforest bird community, although many species decline in abundance and there are changes in community composition. Rare and large-bodied species, and species belonging to the terrestrial insectivore, bark-surface feeder, omnivore, and carnivore diet-guilds appear particularly susceptible to habitat alteration and such species may be targetted for monitoring efforts. Direct intervention in the form of restoration efforts and augmenting of key attributes such as woody plant and cane density and tree species composition may be required for conservation and maintenance of rainforest bird communities in sites that have faced such forms of habitat alteration.

5.6 SUMMARY

The Western Ghats, a global biodiversity hotspot and endemic bird area, has witnessed substantial forest conversion due to plantations and logging. This study examined the effects of alteration of tropical rainforest vegetation structure and composition on bird community structure and the influence of life-history traits on species persistence in the Kalakad-Mundanthurai Tiger Reserve. Systematic sampling for vegetation and point count surveys for birds were carried out in cardamom plantations

abandoned for 5 and 15 years, plantation-rainforest edges, a selectively logged forest patch, and adjoining undisturbed rainforest sites. Principal components analysis of vegetation variables revealed clear differences between undisturbed and altered sites in woody plant and cane densities, canopy cover, and vertical stratification. Bird species richness was lowest in cardamom plantations abandoned for 5 years, intermediate in edges and cardamom plantations abandoned for 15 years, and highest in logged and undisturbed forest. Bird species richness and similarity with undisturbed forest were significantly positively related to the vegetation component representing woody plant and cane densities. Sites that were more similar in tree species composition had more similar bird communities. Similarity in foliage profile and difference in elevation (elevational distance) between sites did not influence bird community similarity. Birds that were rare, large-bodied, and belonging to the terrestrial insectivore, carnivore, omnivore, and bark-surface feeder guilds were adversely affected by habitat alteration. Restoring woody plant and cane densities and rainforest floristic composition in disturbed habitats may be required for management and conservation of bird communities typical to the region.

CHAPTER 6

Effects of fragmentation and plantations on tropical rainforest birds in the Anamalai hills

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CHAPTER 6

Effects of fragmentation and plantations on tropical rainforest birds in the Anamalai hills

6.1 INTRODUCTION

6.1.1 Conservation issue

Habitat fragmentation, defined simply as the reduction in area of habitat and its distribution in smaller and more isolated patches, is one of the most serious conservation issues to emerge worldwide in recent years (Noss and Csuti 1997). This is of critical concern to conservation biologists, particularly in regions with tropical rainforest, which are the greatest living treasuries of biological diversity on Earth (Richards 1996, Wilson 1992), as severe threats and human onslaught also often impinge upon these forests. Estimates reveal that between 1981 and 1990, about 150 million ha of tropical forest (9% of the world's tropical forest) were lost around the world to various forces of deforestation, most (85%) of the area being tropical moist forest, and most previously pristine landscapes now contain only remnant fragments and secondary forests (Brown and Lugo 1990, Myers 1991, Laurance and Bierregaard 1997, Whitmore 1997). This undoubtedly contributes significantly to the present global extinction crisis (Wilson 1992). As large forest tracts are converted to 'islands' in a 'sea' of altered and developed areas, the survival of many plant and animal species will hinge upon their ability to persist in human-modified landscapes and on our direct efforts to conserve and manage these species and their habitats.

The Western Ghats hill ranges of India typify many of these conservation problems. This hill chain is recognised as one of the eight 'hottest hot spots' of biological diversity in the world (Myers *et al.* 2000) and among the 200 globally most important ecoregions (Olson and Dinerstein 1998). Among the global biodiversity hotspots, the Western Ghats and Sri Lanka rank third in terms of the

number of endemic vertebrates/area ratio (species/100 km², Myers *et al.* 2000). For birds, the region has been recognised as an Endemic Bird Area with 16 species of restricted-range birds, including 12 of near-threatened conservation status (Stattersfield *et al.* 1998). According to a recent evaluation, the Western Ghats supports populations of one endangered, three vulnerable, and seven near-threatened bird species, of which all but two inhabit tropical rainforests (BirdLife International 2001).

On the other hand, the Western Ghats faces severe threats from human disturbance due to deforestation, developmental activities, conversion to plantations, and habitat fragmentation (Nair 1991). Menon and Bawa (1997) estimated that between 1920 and 1990 forest cover in the Western Ghats declined by 40%, resulting in a four-fold increase in the number of fragments, and an 83% reduction in size of forest patches. This is not surprising given that this region is one of the biodiversity hotspots with the highest human population density (Cincotta *et al.* 2000).

One of the major causes of forest fragmentation in the Western Ghats is the spread of plantations, particularly tea, coffee, and *Eucalyptus*. The area under plantations is large and growing. The area under tea plantations in the south Indian states increased from 74,765 ha in 1987 to 87,993 ha in 1998. In 1998, this US$ 400 million industry employed over 195,000 people (1999 Statistics of the Tea Board of India). Large areas of *Eucalyptus* plantations also occur with tea as it is used as fuelwood for the factories. Similarly, in 1999–2000, the US$ 500 million Indian coffee industry had plantations over 293,000 ha, almost entirely in southern India. This industry, producing over 170,000 tons of coffee annually and employing over 520,000 people, accounts for substantial non-natural forest canopy cover in the states of Karnataka, Kerala, and Tamil Nadu in the Western Ghats (Coffee Board Statistics 2001).

Recent studies have highlighted continuing threats to tropical rainforest and wildlife species in the Western Ghats (Daniels *et al.* 1995, Kumar *et al.* 1995, Umapathy and Kumar 2000). There is an urgent need to comprehensively study the long-term impacts of such habitat changes and landscape alteration on birds and identify ameliorative conservation measures.

6.2.2 Conceptual background: Species survival in fragmented landscapes

An enormous literature exists on the effects of habitat fragmentation on plant and animal communities in the tropics (see reviews in Saunders *et al.* 1991, Andrén 1994, Simberloff 1994, Wiens 1994, Turner 1996, Turner and Corlett 1996, Laurance and Bierregaard 1997). Although a comprehensive review is impracticable here, a brief mention of the major mechanisms and hypotheses proposed to explain the effects of fragmentation is provided below.

Island biogeography–area and isolation: Early studies that found species richness to be a function of island or fragment area and isolation explained this pattern in relation to the theory of island biogeography (MacArthur and Wilson 1967, Diamond 1975b, 1976, Newmark 1991). Due to

extinction and colonisation dynamics that were a function of species richness, larger or nearer islands were expected to contain a greater number of species than those smaller or further away.

Habitat diversity: Remnant patches do not merely differ in size from larger areas of forest that existed prior to fragmentation. A large number of habitat changes are brought about due to edge effects, microclimatic changes, increased exposure, and human disturbance (Lovejoy *et al.* 1986, Saunders *et al.* 1991). The remnants may also contain only a subset of microhabitats otherwise available in a larger area. Changes in habitat structure or lack of specific microhabitats may be more directly involved in influencing species occurrence or abundance patterns in fragments than other factors (Simberloff 1994). Sites more similar to primary forest in habitat structure and floristics may be expected to contain more similar bird communities (Raman *et al.* 1998).

Landscape matrix effects: Unlike true islands, most forest fragments are not surrounded by a sea of inhospitable or ecologically neutral environments (Wiens 1994). The altered habitats in the surrounding landscape matrix are a source of potential colonists as well as being suitable for colonisation by species that can persist in such habitats. The ability of species to survive in fragments may thus depend on surrounding habitats and whether the species uses such habitats (Stouffer and Bierregaard 1995a,b, Laurance *et al.* 1997, Renjifo 2001).

Differential extinction–nested subsets: Differential extinction of species may lead to the appearance of a nested subset pattern of species occurrence, where successively larger fragments contain species found in all smaller fragments (Patterson and Atmar 1986, Patterson 1987, Bolger *et al.* 1991, Cutler 1991, McCoy and Mushinsky 1994, Worthen 1996, Wright *et al.* 1998). The pattern may be caused by differential extinction vulnerability attributable to density (Bolger *et al.* 1991) or even the nested occurrence of microhabitats used by the species. Although a great majority of published studies report significantly nested patterns of occurrence of species (Wright *et al.* 1998), there has been considerable debate on which methods are appropriate to assess nested subset structure (Cutler 1991, Simberloff and Martin 1991, Cook and Quinn 1998, Worthen 1996, Brualdi and Sanderson 1999, Cam *et al.* 2000). In addition, contrasting patterns of nested subset structure may be shown by different ecological groups of species (Kadmon 1995, Fleishman and Murphy 1999) or in relation to different independent variables such as species richness, area, or isolation (Simberloff and Martin 1991, Kadmon 1995).

Species attributes: The response of birds to fragmentation may depend on specific life-history attributes. Species groups that may be particularly susceptible include large-bodied frugivores and carnivores (Leck 1979, Terborgh and Winter 1980, Brash 1987, Thiollay 1989, Kattan *et al.* 1994), and terrestrial and understorey insectivores (Leck 1979, Stouffer and Bierregaard 1995a, Canaday 1996, Stratford and Stouffer 1999). Other factors that are known to increase

vulnerability include high population variability (Karr 1982) and restricted range (Simberloff 1994).

Random sampling: In exploring the effects of fragmentation, it is necessary to test the possibility that the observed patterns may have arisen by chance alone. One mechanism that may produce a positive relationship between species richness and area is random colonisation of fragments, depending on their area (Coleman *et al.* 1982) and/or isolation (Hubbell 2001). As larger fragments are likely to contain more individuals, greater species richness is expected by chance alone (Wiens 1989, Haila *et al.* 1993, Villard *et al.* 1995).

6.2 OBJECTIVES

This study aimed at understanding the relative influence of the above multiplicity of factors proposed to explain the effects of forest fragmentation and habitat alteration on bird communities. The major questions addressed during the study were:

1. Are bird species richness and abundance predictable from fragment area and isolation (as expected under island biogeography theory), habitat attributes (habitat structure and diversity hypothesis), or from null models that simulate random colonisation or assembly of species (passive sampling)?

2. What is the pattern of species turnover across fragments? Is species composition and turnover correlated with site and habitat characteristics? Do smaller fragments contain "nested-subsets" of species occurring in larger fragments due to differential species colonisation or extinction?

3. Are birds that avoid altered habitats (plantations) in the surrounding landscape matrix more susceptible to habitat fragmentation than more generalist species?

4. How do different diet-guilds and species categories of birds respond to habitat fragmentation? What is the conservation status of endemic and rare bird species and are they more vulnerable to habitat fragmentation and conversion than other species?

6.3 METHODS

6.3.1 Selection of sampling sites

The area chosen for study was the highly man-altered landscape of the Anamalai hill ranges in the southern Western Ghats. Details of the Anamalai hills, where this part of the study was carried out, are provided in Chapter 2. Following Umapathy and Kumar (2000), for the purposes of this study, fragments were defined as patches of relatively intact or degraded tropical evergreen forest that were

isolated (except for very narrow corridors, if any) from other such patches by being surrounded by other vegetation types, plantations, reservoirs, or human habitation. Birds were sampled using point counts in 13 rainforest fragments ranging in size from 0.3 ha to 2,600 ha and the matrix of tea (*Camellia sinensis*), coffee (*Coffea arabica*), and *Eucalyptus* plantations in the Valparai plateau and Indira Gandhi Wildlife Sanctuary (Plate 3, Figure 2.5, Table 6.1). Eleven fragments were in an altitudinal range of 800 to 1,400 m altitude in mid-elevation tropical evergreen forest (*Cullenia-Mesua-Palaquium* type), while the other two (Karian Shola and Varagaliar) occurred at a slightly lower elevation.

Table 6.1: Area, location, and matrix surrounding rainforest fragments sampled in the Anamalai hills.

Fragment	Area (ha)	Location	Altitude[a] (m)	Matrix[b]
Kochank 2 (K2)	0.3	76° 56′ 35″ - 10° 19′ 27″	1,050	T, E
Kochank 1 (K1)	0.5	76° 56′ 43″ - 10° 19′ 20″	1,053	T
Varattuparai 4 (V4)	1	76° 55′ 43″ - 10° 21′ 21″	1,020	T, C, R
Varattuparai 1-3 (V3)	7	76° 55′ 48″ - 10° 21′ 21″	1,025	T, C, H
Pannimade (PA)	10	76° 53′ 42″ - 10° 17′ 46″	1,044	T, C, R
Tata Finley (TF)	24	76° 56′ 3″ - 10° 20′ 55″	1,023	C, E, H
Korangumudi (KO)	35	76° 54′ 45″ - 10° 18′ 50″	1,040	C, T, H
Puthutotam (PU)	50	76° 58′ 2″ - 10° 20′ 28″	1,144	C, T, H
Andiparai (AN)	185	76° 59′ 36″ - 10° 23′ 39″	1,295	T, H
Manamboli (MA)	200	76° 53′ 44″ - 10° 21′ 11″	813	C, D
Karian Shola (KS)	650	76° 50′ 0″ - 10° 28′ 34″	807	D, B
Varagaliar (VA)	2,000	76° 51′ 56″ - 10° 25′ 4″	681	D, B
Iyerpadi-Akkamalai (IYAK)	2,600	77° 00′ 28″ - 10° 20′ 57″	1,354	T, H, G

[a] Average of readings taken at sampling points as described in Methods.
[b] E - *Eucalyptus*, C - coffee, T - tea, R - reservoir, H - Human habitation, D – Moist and dry deciduous forests, B - Bamboo, G - Grassland.

Areas of fragments were obtained from Kumar *et al.* (1995) and Umapathy and Kumar (2000) and, in some cases, company records or direct on-field measurements of smaller fragments. Fragments had roads passing through or adjacent to them; Pannimade was the only fragment over 100 m away from any main road. One of the study sites (Varattuparai 1–3), considered as three separate fragments in the earlier publications, was considered as single fragment during this study. A small road and a border strip clearing separate the three portions of this fragment. All sorts of birds, including understorey and canopy species, were seen crossing these narrow openings and, from the perspective of birds, these sites were effectively parts of a single fragment. Similarly, Iyerpadi and Akkamalai, although cut by a road towards the northern periphery, are essentially one contiguous patch for the highly vagile birds, and are therefore considered as a single fragment (Iyerpadi-Akkamalai complex) for this study. As this was the largest patch in this altitudinal range, and being relatively undisturbed and lying within the Indira Gandhi Wildlife Sanctuary, it was also used as a 'control' site against which other fragments are compared in some analyses. This patch, however, did not range into elevations below 1,200 m and lacked many typical low-elevation bird species (see Chapter 4). I therefore sampled three fragments at lower elevations (spanning 650 m to 1,000 m),

including a very large fragment (Varagaliar, 2,000 ha), a large fragment (Karian Shola, 650 ha), and a medium-sized fragment (Manamboli, 200 ha).

6.3.2 Bird surveys

The fixed-radius point count method was used to survey bird populations in each site. A radius of 50 m and duration of 5 min was used. Details of the method are presented in Chapter 3. No two points sampled on the same day were closer than 100 m to avoid overlap. Points sampled on different days unavoidably overlapped to some extent in the smaller fragments.

A total of 389 point count samples were obtained across the 13 fragments between January and May 2000, spanning the peak breeding season and the period when winter migrants are present in the study area. Bird surveys were designed upon two major needs, but were limited by two main constraints. The primary need was to sample all sites in a relatively uniform and efficient manner during the main breeding season. In addition, there was a need to distribute sampling effort (number of point count surveys at a site) in relation to fragment size for comparisons of species richness. This ideal sampling scheme was not possible due to two constraints. First, although all fragments were sampled using the same methods and over the same period of time, for logistic reasons, two of the lower-elevation fragments could be sampled mainly towards the end of the breeding season. The sampling in proportion to area criterion was also impossible to adhere to since, for every additional point count survey in a 1 ha fragment, 2,600 point count samples would be needed in the largest fragment sampled in this study (Iyerpadi-Akkamalai, 2,600 ha). Although, in general, more samples were taken in larger fragments, this was not exactly proportional to fragment area, and larger fragments tended to be sampled less intensively than smaller fragments. Besides this, detectability and visibility tended to be better in small and medium-sized fragments (except Pannimade). As a result of these two factors (disproportionate sampling and detectability), the species richness of large fragments may be underestimated and the results of the study can therefore be only considered as a conservative assessment of the effects of fragmentation.

One site was chosen in each of the three following types of plantations that were most common in the landscape matrix around rainforest fragments: tea, coffee, and *Eucalyptus*. In each of these three sites, 25 point count surveys were carried out. It was not possible to sample additional sites or choose sites to make specific comparisons between fragments surrounded by different kinds of matrix elements during this study.

6.3.3 Habitat sampling

In each of the 13 rainforest fragment and 3 plantation sites, a number of vegetation variables were measured in order to characterise habitat structure and floristic composition of the sites. Tree (>30 cm girth at breast height) densities were estimated using the point-centred quarter method (PCQ, Krebs

1989). From 10 to 30 plots were measured depending on the size of the fragment (25 plots in plantations). In three of the smaller fragments that had very dense tangled undergrowth it was difficult to do PCQ plots and therefore trees within ten 5-m radius circles around the observer were counted to estimate density. In most cases, trees were identified to species using available floras and field guides (Gamble 1935, Pascal and Ramesh 1997). A number of species were identified to genus level and given code numbers; the few trees that remained unidentified were pooled into a single category.

Other habitat variables were measured at 25 points in each fragment or plantation site distributed over areas where bird surveys were carried out. Altitude was measured using an altimeter (10 m accuracy). Other variables (percentage canopy cover, canopy height, vertical stratification, leaf litter depth, shrub and cane densities) were measured as described earlier (Chapters 4, 5). Care was taken to avoid locating sampling points in the centre of highly disturbed trails, most samples were taken at least 10 m into the forest interior. The latitude and longitude of each sampling site (to the nearest 0.5") was obtained using a hand-held global positioning system (Garmin GPS 12 XL). For large fragments, a reading was obtained close to the centre of the fragment or, in two cases of elongated fragments, readings were obtained at the two ends and averaged to obtain a location that fell close to the centre of the fragment.

6.3.4 Analysis

6.3.4.1 *Bird community parameters*

The 106 bird species recorded during the study were classified into rainforest and open-country (non-rainforest birds). The rainforest species included birds that normally occurred even in mature undisturbed rainforests in Anamalais, KMTR (Chapter 4), and other rainforest areas in the Western Ghats (Ali and Ripley 1983). In contrast, open-country species were birds that never occurred in mature, undisturbed tropical rainforest and occurred only in disturbed rainforest fragments or in naturally drier and open habitats. All analyses were performed using all species, using only rainforest species, and with only open-country species.

Bird species richness (average per point count sample and cumulative number of species recorded) in each site was a fundamental variable of interest. The average bird abundance per point was a second major parameter of interest. In each point count sample, many bird detections were made by calls and the number of individual birds could not be counted in the field. For each species, however, information on flock sizes (a flock representing one to many individuals for this purpose) was collected separately during surveys and opportunistic observations. For each aural detection of a species, the number of individuals in the flock was randomly selected using a Monte-Carlo procedure. More details on flock size data collection and use are given in Chapter 3. This procedure enabled the estimation of the number of individuals in each point count sample.

Cumulative species richness and abundance (individuals/ha) of birds belonging to eight different diet-guilds were also estimated using the point count survey data. Birds were classified as bark-surface feeders, carnivores, frugivores, nectarivore-insectivores, omnivores, and canopy, understorey, and terrestrial insectivores, using natural history information in Ali and Ripley (1983) and direct observations. The species-abundance data from each site was used to estimate similarities between sites in bird community composition using the Morisita index (Wolda 1981). Guild and similarity analyses were done separately for all, rainforest, and open-country species separately.

6.3.4.2 *Habitat variables*

Tree densities and basal areas were computed for each site using data from the PCQ or circular plots. For other variables measured at replicate points in each site (such as shrub density or canopy cover) the averages across points were calculated. Vertical stratification was measured as the average number of vertical strata with foliage at each point. As these measurements were taken at different points, the coefficient of variation of this index was used as a measure of horizontal heterogeneity (Raman *et al.* 1998). As several vegetation variables were inter-correlated, they were summarised using principal components analyses to extract fewer uncorrelated components that described the vegetation gradient.

The latitude-longitude location data of each site were converted to X- and Y-coordinates (in metres) using 1" = 30.867 m as a conversion factor. The distance between any two sites as well as the distance from each site to the Iyerpadi-Akkamalai 'control' site was then estimated. This was used as a measure of isolation of fragments from the putative source area for some analyses.

6.3.4.3 *Relationships between birds, habitat, area, and isolation*

The influence and relative importance of area, isolation, altitude, and habitat (represented by the principal component scores) on bird community attributes was examined using stepwise multiple regression (Zar 1999). Stepwise regression analyses were also carried to examine the influence of these variables on the number of bird species in eight different diet-guilds and within different defined categories of birds such as migrants, endemic species, and priority species. Priority species were defined as birds of restricted-range (Stattersfield *et al.* 1998), discontinuous distribution (in rainforests of southwest India, Sri Lanka, and northeast India, Ali and Ripley 1983), or near-threatened (Collar *et al.* 1994) and did not include endemic species. The expected species richness of each site was examined in relation to two random sample null models that modelled the effects of random colonisation (passive sampling) of sites by bird species. The two models used were:

(a) **Area-based passive sampling:** This is the model of Coleman *et al.* (1982), where an individual has a greater probability of colonising large rather than small fragments. Specifically, the probability of a bird occurring at a site was taken to be the proportional area of the site (p_{area} = area of site/total area summed across all sites). Thus, the probability that at least one individual of a species *i* occurs in

a site is given by $[1 - (1 - p_{area})^{ni}]$, where *ni* is the total number of individuals of species *i* recorded across all sites. The expected species richness is the summation of this probability across all species:

$$S_{area} = \sum_{i=1}^{S_p} [1 - (1 - p_{area})^{ni}]$$

Using the binomial distribution, the variance of S_{area} is given by (Coleman *et al.* 1982):

$$V_{area} = \sum_{i=1}^{S_p} (1 - p_{area})^{ni} - \sum_{i=1}^{S_p} (1 - p_{area})^{2ni}$$

This model was found by Coleman *et al.* (1982) to predict breeding bird species richness on islands in the Pymatuning lake in North America and by Haila *et al.* (1993) for breeding birds in the Finnish Taiga. This model often results in virtually all individuals 'gathering' in the largest fragment (2,600 ha in this study, p_{area} = 0.451) while small ones receive very few individuals due to their small proportional area (K2 = 0.30 ha, p_{area} = 0.005). As the data gathered were from sampling that was not exactly proportional to area, this model was unsuitable for application in this study. A modified version of the model was therefore used.

(b) **Abundance-based passive sampling:** The Coleman *et al.* (1982) model was modified to predict the expected species richness under the situation where the actual number of individuals seen on an island was randomly sampled from the entire pool of individuals summed across all sites. The probability of colonisation was thus taken to be the proportion of individuals sampled in a given site (p_{abun} = number of individuals in a site/total number of individuals recorded across all sites). Again, the expected species richness under abundance-based passive sampling is:

$$S_{abun} = \sum_{i=1}^{S_p} [1 - (1 - p_{abun})^{ni}]$$

And the variance is given by:

$$V_{abun} = \sum_{i=1}^{S_p} (1 - p_{abun})^{ni} - \sum_{i=1}^{S_p} (1 - p_{abun})^{2ni}$$

6.3.4.4 *Species turnover and nested subset analyses*

Similarities between sites in bird community and tree species composition were measured using the Morisita index that is least sensitive to sample size effects (Wolda 1981). Dissimilarities were measured as 1 - Morisita index. Dissimilarity between sites in habitat structure was estimated as the Euclidean distance between sites in the PC1-PC2 ordination space. The altitudinal and geographic distances between sites were also calculated. The difference in the logarithms of the area of the sites

was taken as a measure of dissimilarity in fragment size. The influence of dissimilarities between sites in area, location, habitat structure, and tree species composition, on the dissimilarities in bird community composition was assessed using stepwise multiple regression analyses.

The pattern of nested subsets or nestedness is defined by the condition that as one proceeds from sites containing the most species to the fewest species, the species drop out, not at random, but in a specific progression such that each site is a subset of each preceding site (Patterson and Atmar 1986). Nested subset structure of assemblages can reflect several different underlying processes such as differential colonisation, differential extinction, nested habitats, and passive sampling effects (see Worthen 1996, Wright *et al.* 1998 for reviews). Nestedness analyses are of great relevance for conservation for two main reasons. First, it would imply that community composition changes in a predictable manner and a set of small fragments would tend to contain more or less the same set of species, forming a subset of what is found in richer, larger fragments (Patterson 1987, Worthen 1996). Second, it helps identify patterns of differential extinction and species that are susceptible to extinction with decrease in fragment size or species richness.

It is not possible to address in detail in this chapter the different methods of nested subsets analyses. For the purpose of the present thesis, I use the analytical approach of Atmar and Patterson (1993) to determine nestedness. Starting with a presence-absence matrix of sites (rows) by species (columns), their nestedness calculator estimates an index of nestedness, called the matrix temperature, after maximally packing the matrix (presences cluster at the top left). The null distribution of matrix temperatures is calculated after similarly packing simulated matrices generated by distributing the observed number of presences at random in the matrix. Statistical significance was assessed using the tail probabilities of the simulated distribution (1,000 simulations).

6.4 RESULTS

In the 13 rainforest fragments, 4077 detections of birds were obtained, comprising of an estimated 7493 individuals in total (Appendix 4). Of the 106 bird species observed in this sample, 75 species (70.8%) were birds typical of rainforest (e.g., Great Hornbill, Malabar Trogon, Black-and-Orange Flycatcher). The remaining 31 species (29.2%) were typical of drier forests, forest edges, and degraded open areas of the Indian Peninsula, and included mostly common and widespread species (e.g., Common Tailorbird, Red-vented Bulbul, House Crow).

In addition, 449 detections comprising of an estimated 792 individual birds were made in tea, coffee, and *Eucalyptus* plantations. A total of 61 species was recorded in this sample, including 34 rainforest species (55.7%) and 27 open-country species (44.3%). While all 34 rainforest species were also detected in fragments, two of the open-country species (Pied Bushchat and Long-tailed Shrike) were not seen in rainforest fragments. Of the 47 bird species recorded in rainforest fragments but absent in the plantations, 41 (87.2%) were rainforest birds and 6 (12.8%) were open-country species.

6.4.1 Bird species richness and abundance in rainforest fragments

Bird species richness and abundance data were obtained from unequal sampling effort distributed across the 13 sites (Table 6.2). The number of point counts/ha, a measure of sampling intensity, ranged from 13-14 in the smallest fragments to less than 0.1 in the largest for reasons explained in the section on methods (section 6.3.3). In most cases, particularly in medium-sized fragments, the species richness appeared to have levelled off at near-saturation point reflecting adequate sampling effort. In the smallest fragments, few counts were carried out and 1 or 2 additional species were detected even in the last sample count, indicating that more species may be recorded. Field observation indicated that many of these detections were of birds that flew into the fragment from an adjacent site, perched for a few moments, and flew out again, and therefore using the site ephemerally. In the largest fragments also, a few additional species were being detected in the last few counts, and these appeared to be instrinsically rare and typical rainforest birds such as frogmouths, forest raptors, and owls.

Table 6.2: Sampling effort in the rainforest fragments in the Anamalai hills.

Fragment	Area (ha)	Relative area (%)	Number of point counts	Relative counts (%)	Sampling intensity (point counts/ha)
Kochank 1 (K1)	0.3	0.0052	4	1.03	13.33
Kochank 2 (K2)	0.5	0.0087	7	1.80	14.00
Varattuparai 4 (V4)	1	0.0174	6	1.54	6.00
Varattuparai 1-3 (V3)	7	0.1215	20	5.14	2.86
Pannimade (PA)	10	0.1735	30	7.71	3.00
Tata Finley (TF)	24	0.4165	30	7.71	1.25
Korangumudi (KO)	35	0.6073	30	7.71	0.86
Puthutotam (PU)	50	0.8676	30	7.71	0.60
Andiparai (AN)	185	3.2102	42	10.80	0.23
Manamboli (MA)	200	3.4705	45	11.57	0.23
Karian Shola (KS)	650	11.2792	40	10.28	0.06
Varagaliar (VA)	2,000	34.7054	30	7.71	0.02
Iyerpadi-Akkamalai (IYAK)	2,600	45.1170	75	19.28	0.03

6.4.1.1 *Trends in bird species richness, abundance, and population sizes*

Bird species richness changed from the smallest to the largest fragments in different ways depending on which set of species was considered. The total species richness increased from about 20-30 species in the small fragments (<10 ha) to over 50 species in the medium-sized fragments (30-50 ha), and then remained steady or declined slightly towards the largest fragments (Figure 6.1a). Open-country birds contributed substantially (up to about 40%) to the species richness of small and medium fragments. The number of open-country bird species declined with fragment size, being highest however in one highly disturbed medium-sized fragment, Korangumudi (Figure 6.1b). In contrast, the number of typical rainforest bird species increased with fragment size (Figure 6.1c). Even here, however, the species richness was lowest only below a threshold of 10 ha, and medium-sized fragments had nearly 80% of the species that the largest fragments had (Figure 6.1c). It must be noted

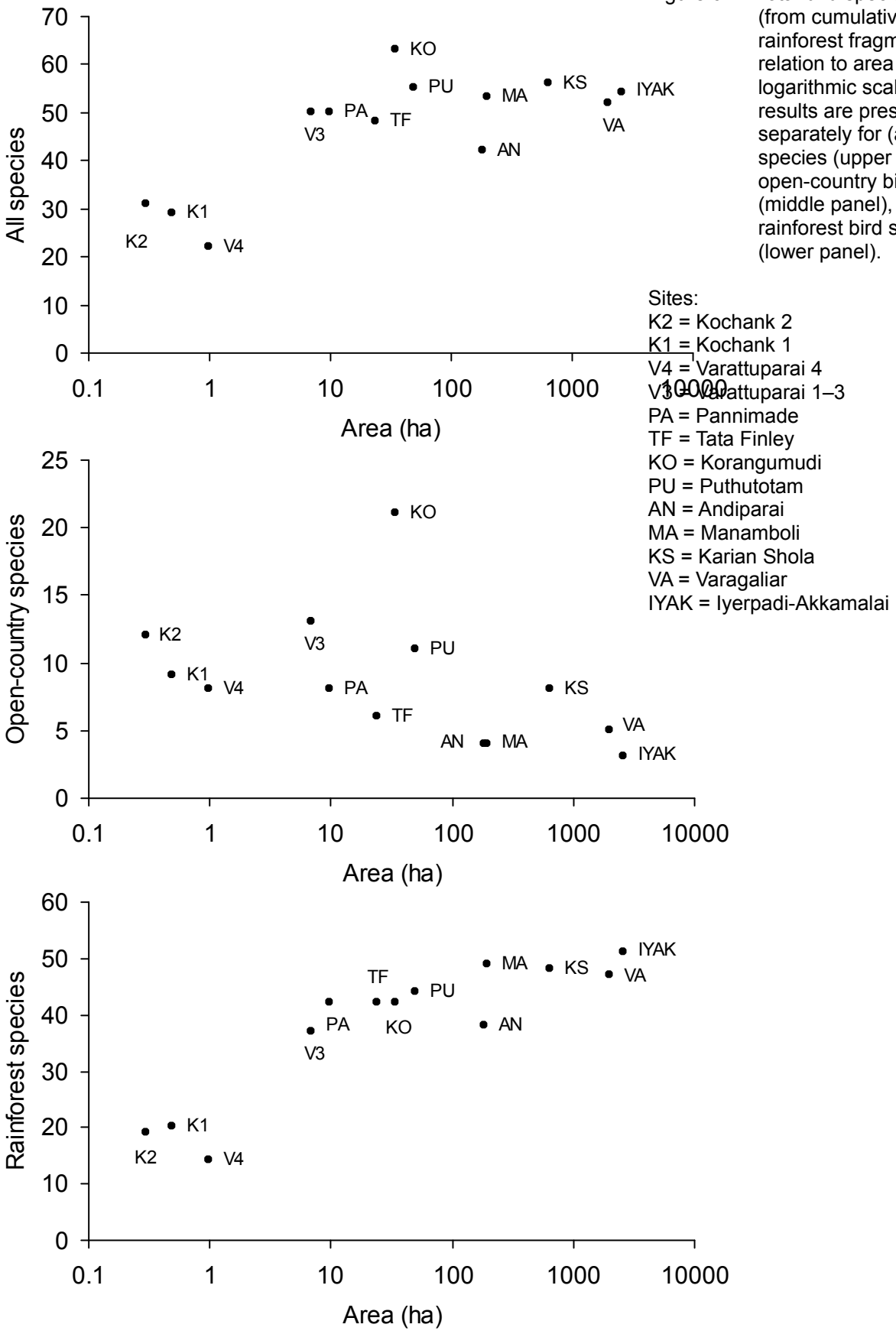

Figure 6.1: Total bird species richness (from cumulative list) of rainforest fragments in relation to area on a logarithmic scale. The results are presented separately for (a) all bird species (upper panel), (b) open-country bird species (middle panel), and (c) rainforest bird species (lower panel).

Sites:
K2 = Kochank 2
K1 = Kochank 1
V4 = Varattuparai 4
V3 = Varattuparai 1–3
PA = Pannimade
TF = Tata Finley
KO = Korangumudi
PU = Puthutotam
AN = Andiparai
MA = Manamboli
KS = Karian Shola
VA = Varagaliar
IYAK = Iyerpadi-Akkamalai

that this discrepancy may have been higher if sampling intensity had been equal across sites. When the total number of resident bird species in fragments was considered, the patterns were nearly identical (Figure 6.2a-c).

The pattern of bird species richness recorded per point showed an interestingly different trend with fragment area. The average number of bird species per point did not change significantly or show any discernible trend with fragment size (Figure 6.3a). Again, however, the number of open-country species recorded per point was higher is small and medium-sized fragments, declining to negligible values in the largest fragments (Figure 6.3b). In contrast, the species richness per point of typical rainforest birds increased with fragment size, from smallest to the largest (Figure 6.3c). Notably however, the highest bird species richness per point was recorded in Pannimade, a small fragment with relatively well-preserved rainforest vegetation and low level of disturbance.

The pattern of change in bird abundance per point was also virtually identical to that shown by bird species richness per point, due to the obvious correlation between these variables (Figure 6.4a-c). Again, Pannimade had one of the highest values, with an average of 21 individual rainforest birds recorded in each point count.

These patterns are reinforced by regression and correlation analyses of the above data. Among a variety of models explored, two appeared to fit the data best—log-linear and log-polynomial models—the results of which are presented in Table 6.3. The log-polynomial models perform better (R^2 = 71-74%) than log-linear models (R^2 = 46-53%) in describing the pattern of total and resident bird species richness for all species combined. This inverse-U shaped relationship is because of the peak in species richness in medium-sized fragments. For open-country and rainforest bird species, the log-linear models perform nearly as well as the log-polynomial, indicating trajectories of decline and increase in species richness with area, respectively (Table 6.3, Figures 6.1, 6.2, 6.3, 6.4). The statistical significance of the relationships with fragment area is indicated by the Kendall rank-order correlation coefficients in Table 6.3.

Although a sizable number of rainforest bird species were recorded in small and medium-sized fragments, their population sizes (estimated as the product of individual densities and fragment area) were very small. None of the fragments less than 10 ha in area had any bird species represented by 10 or more individuals in the fragment (Table 6.4). Medium-sized fragments (10-100 ha) contained populations of over 10 to over 50 individuals of more than two dozen rainforest bird species. Large populations of over 100 individuals of any rainforest bird species were, however, recorded only in large fragments (>100 ha, Table 6.4). However, (i) most species (>94%) recorded in the smallest fragments (<1 ha) were transients with populations of less than 1 individual in the site, as it is virtually impossible for any species to be resident and entirely confined to such small areas, and (ii) many species (6-22%) were recorded as having population sizes of <1 individual even in medium and large-sized fragments (Table 6.4). The latter is partly due to sampling effects (see Discussion).

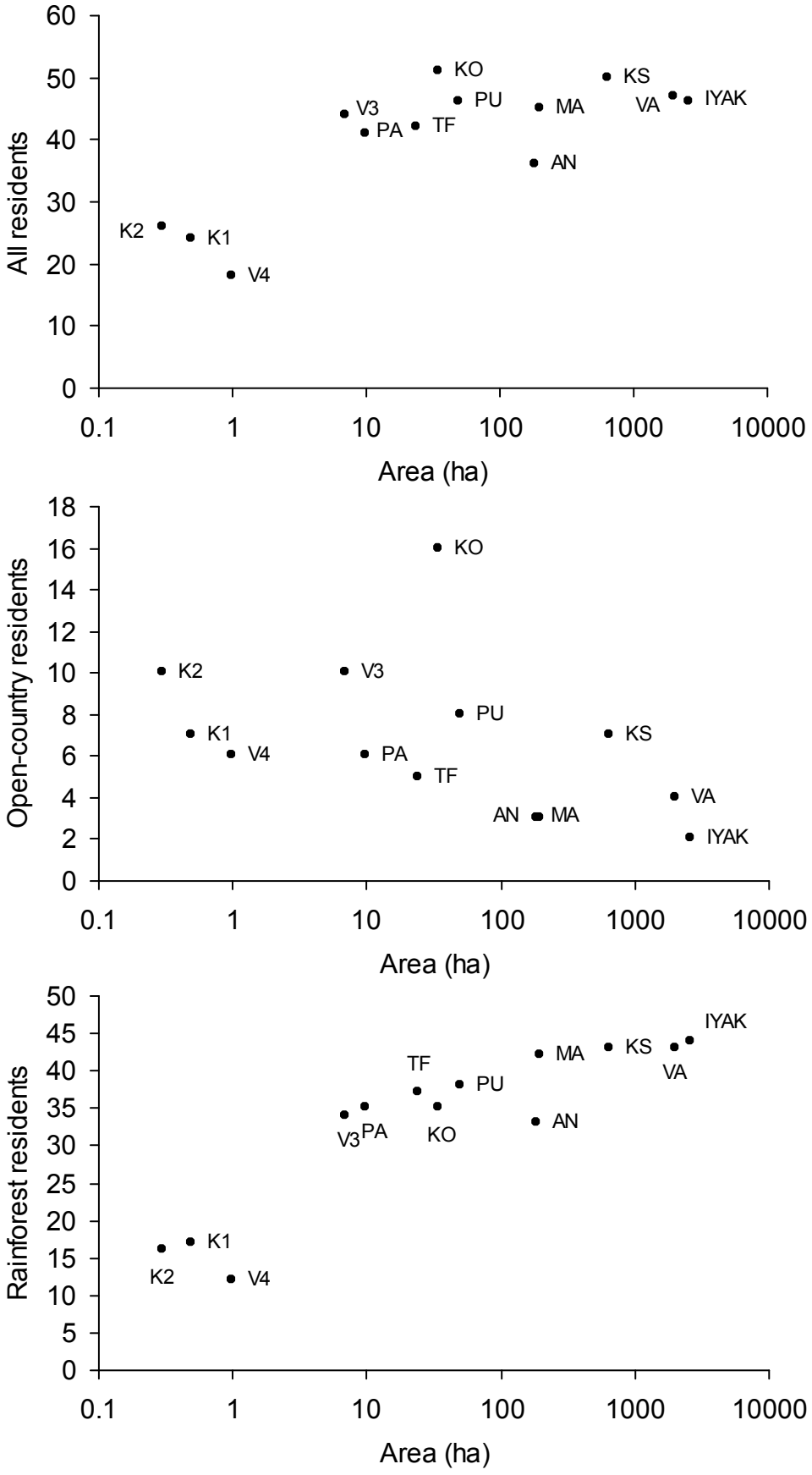

Figure 6.2: Total resident bird species richness (from cumulative list) of rainforest fragments in relation to area on a logarithmic scale. The results are presented separately for (a) all bird species (upper panel), (b) open-country bird species (middle panel), and (c) rainforest bird species (lower panel). Site names as in Figure 6.1.

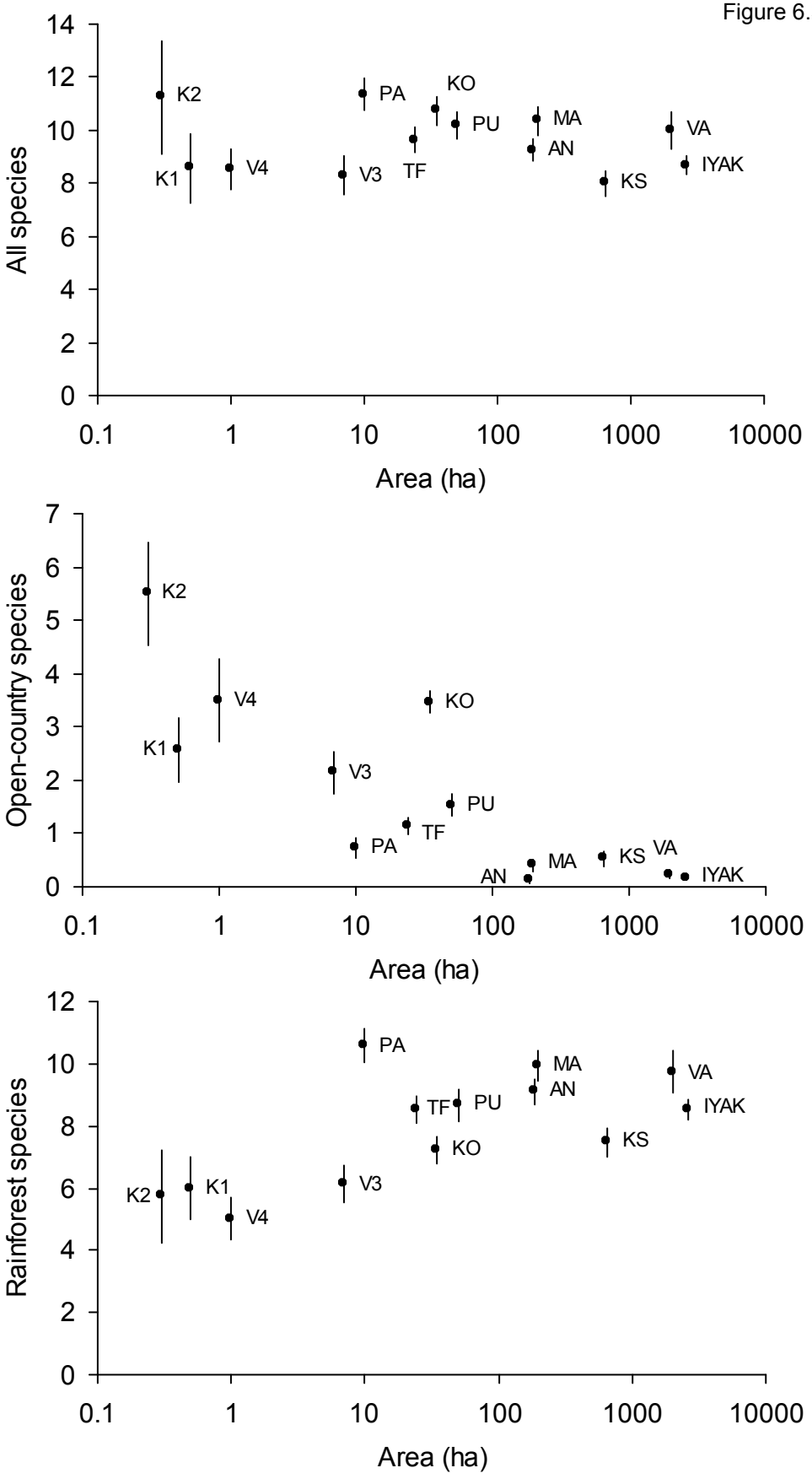

Figure 6.3: Bird species richness per point count (mean ± SE) of rainforest fragments in relation to area on a logarithmic scale. The results are presented separately for (a) all bird species (upper panel), (b) open-country bird species (middle panel), and (c) rainforest bird species (lower panel). Site names as in Figure 6.1.

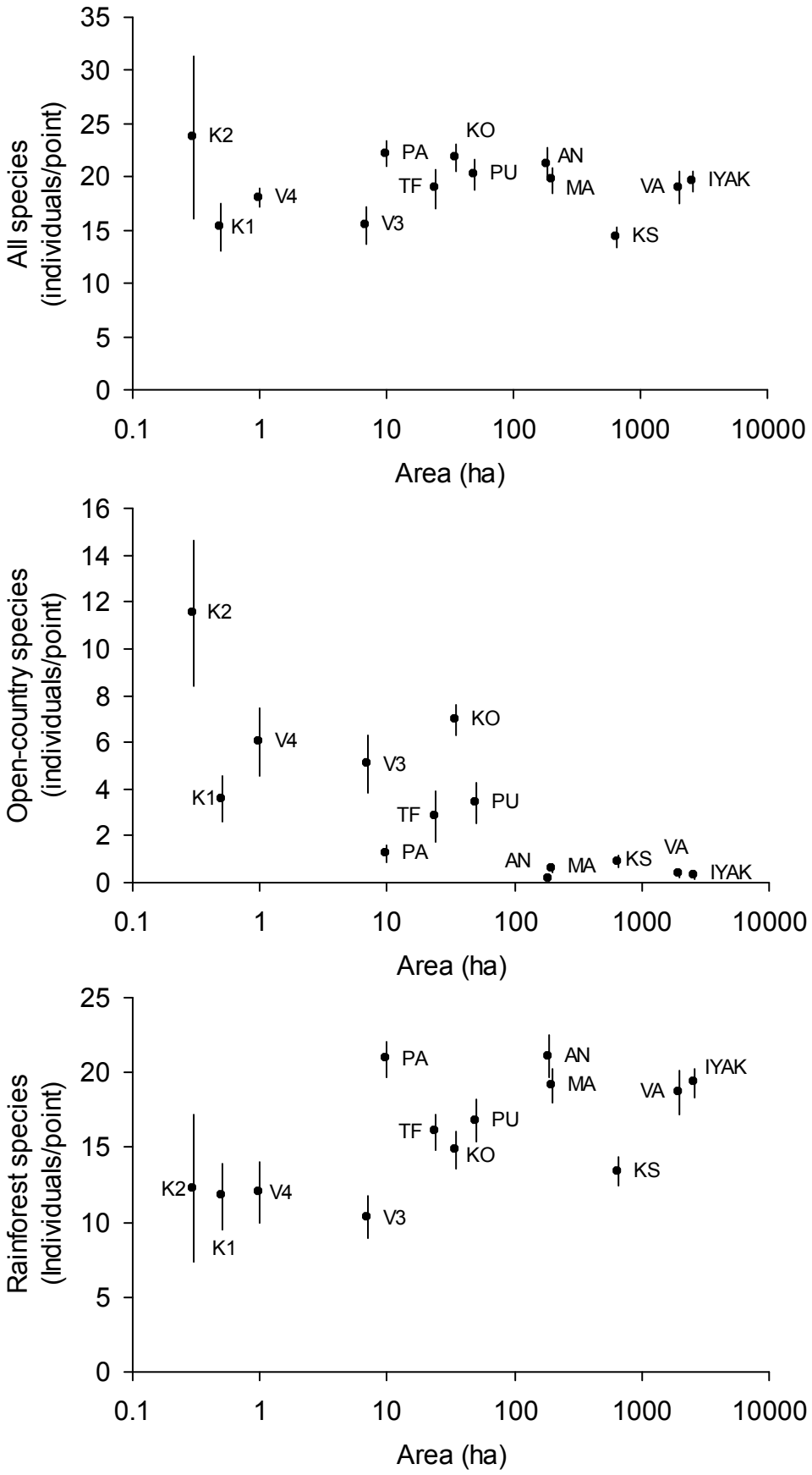

Figure 6.4: Bird abundance per point (mean ± SE) in the rainforest fragments in relation to area on a logarithmic scale. The results are presented separately for (a) all bird species (upper panel), (b) open-country bird species (middle panel), and (c) rainforest bird species (lower panel). Site names as in Figure 6.1.

Table 6.3: Regression models and non-parametric Kendall correlations of data relating bird species richness and abundance estimates (y) to the logarithm of the area [x = log (area)] of fragments in the Anamalai hills.

Parameter	Linear[a] ($y = bx + c$)			Polynomial[a] ($y = ax^2 + bx + c$)				Kendall correlation
	b	c	R^2 (%)	a	b	c	R^2 (%)	τ
Total bird species richness								
All species	7.25	34.67	45.9	-5.45	26.05	24.42	71.0	0.45*
Open-country species	-1.997	11.89	21.5	-1.17	2.05	9.79	28.6	-0.50*
Rainforest species	9.24	22.78	72.2	-4.27	23.998	15.13	87.2	0.75**
Resident bird species richness								
All species	6.80	28.55	53.1	-4.32	21.73	20.81	73.8	0.50*
Open-country species	-1.56	9.26	22.1	-0.82	1.24	7.80	27.9	-0.47*
Rainforest species	8.37	19.28	74.9	-3.51	20.48	13.00	87.6	0.78**
Bird species richness/point								
All species	-0.15	9.84	2.2	-0.26	0.75	9.38	8.7	-0.13
Open-country species	-1.15	3.58	61.2	0.35	-2.37	4.21	66.8	-0.67**
Rainforest species	0.998	6.26	40.3	-0.61	3.11	5.17	54.9	0.49*
Bird abundance/point								
All species	-0.16	19.43	0.4	-0.35	1.03	18.81	2.26	-0.08
Open-country species	-2.19	6.89	54.1	0.48	-3.85	7.75	56.6	-0.62**
Rainforest species	2.03	12.55	38.1	-0.83	4.89	11.06	44.2	0.43*

[a]—Models log-linear and log-polynomial in relation to area of the fragment because x = log(area).
*–P < 0.05, **–P < 0.01, ***–P < 0.001 (N = 13 fragments)

Table 6.4: Population sizes of rainforest bird species in fragments in the Anamalai hills.

Population size[a]	Number of species in fragment[b]												
	K2	K1	V4	V3	PA	TF	KO	PU	AN	MA	KS	VA	IYAK
At least 1 bird	1	1	7	24	39	42	42	44	38	49	48	47	51
At least 2 birds	–	–	2	15	31	40	38	44	38	49	48	47	51
At least 5 birds	–	–	–	6	14	27	29	32	38	49	48	47	51
At least 10 birds	–	–	–	–	8	17	21	24	36	45	48	47	51
At least 25 birds	–	–	–	–	1	5	9	16	27	37	39	47	51
At least 50 birds	–	–	–	–	–	1	1	9	21	31	32	47	46
At least 100 birds	–	–	–	–	–	–	1	–	13	18	30	42	43
At least 500 birds	–	–	–	–	–	–	–	–	2	1	5	28	26
At least 1000 birds	–	–	–	–	–	–	–	–	1	–	1	17	18
	Percentage of species in fragment												
At least 1 bird	5.3	3.4	31.8	48.0	78.0	87.5	66.7	80.0	90.5	92.5	85.7	90.4	94.4
At least 2 birds	–	–	9.1	30.0	62.0	83.3	60.3	80.0	90.5	92.5	85.7	90.4	94.4
At least 5 birds	–	–	–	12.0	28.0	56.3	46.0	58.2	90.5	92.5	85.7	90.4	94.4
At least 10 birds	–	–	–	–	16.0	35.4	33.3	43.6	85.7	84.9	85.7	90.4	94.4
At least 25 birds	–	–	–	–	2.0	10.4	14.3	29.1	64.3	69.8	69.6	90.4	94.4
At least 50 birds	–	–	–	–	–	2.1	1.6	16.4	50.0	58.5	57.1	90.4	85.2
At least 100 birds	–	–	–	–	–	–	1.6	–	31.0	34.0	53.6	80.8	79.6
At least 500 birds	–	–	–	–	–	–	–	–	4.8	1.9	8.9	53.8	48.1
At least 1000 birds	–	–	–	–	–	–	–	–	2.4	0.0	1.8	32.7	33.3
Rainforest BSR[c]	19	29	22	50	50	48	63	55	42	53	56	52	54

[a]—Number of individual birds (estimated as density x fragment area)
[b]—Fragment codes as in Table 6.1
[c]–Number of rainforest bird species recorded in fragment

6.4.1.2 *Can bird species richness patterns be explained by passive sampling?*

The hypothesis that bird species richness in fragments was a result of passive sampling in relation to fragment area was not supported by the analysis. Under this model, the large fragments were expected to have more species than observed, whereas the smaller fragments were expected to have fewer species than observed. The pattern was consistent irrespective of whether the analysis included all, open-country, or rainforest species. For reasons mentioned in Methods (6.3.4.3a) these results are only suggestive and a more appropriate test is the abundance-based passive sampling model.

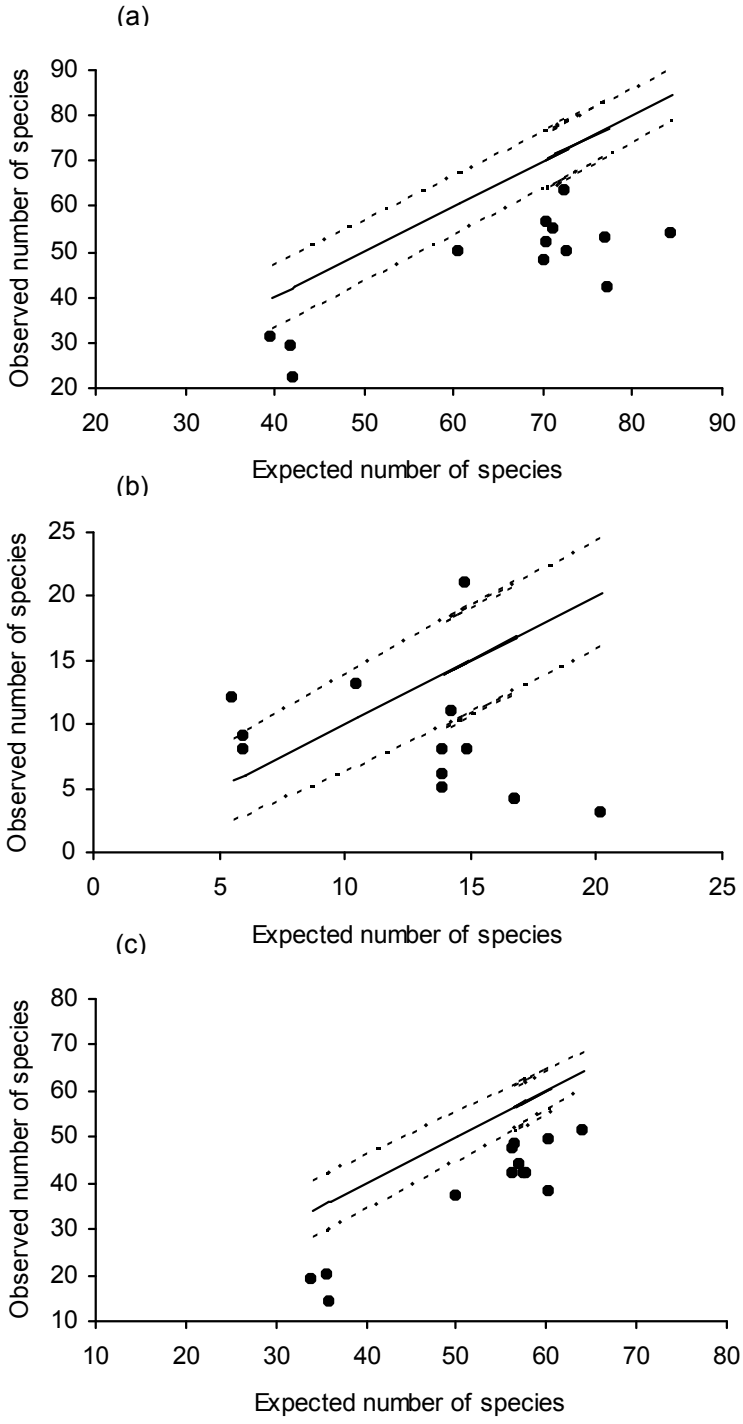

Figure 6.5: Expected bird species richness from passive sampling models in relation to observed bird species richness in rainforest fragments in the Anamalai hills. Results of abundance-based passive sampling for:
(a) all species,
(b) open-country species, and
(c) rainforest species.

The abundance-based passive sampling also did not generally predict the bird species richness, but gave some illuminating insights. When all species were considered, the number of bird species expected in each site was generally higher than actually observed (Figure 6.5a). The discrepancy was highest for the largest fragments, with smaller fragments (that had fewer species) having only slightly less than expected. In contrast, when open-country bird species are examined, the larger fragments had far fewer species than expected whereas some small and medium-sized fragments had species richness values falling within the expected interval (Figure 6.5b). Notably, the highly disturbed rainforest fragment, Korangumudi, had the highest number (21) of open-country bird species. The analysis of rainforest bird species alone revealed a pattern (Figure 6.5c) similar to that of all species (Figure 6.5a). The three smallest fragments seemed to have, however, disproportionately (44 - 61%) fewer rainforest species than expected, in comparison to the three largest fragments (15 - 21% fewer species than expected, Figure 6.5c).

6.4.1.3 *Changes in vegetation and habitat structure*

As a prelude to analysing the effects of habitat structure, area, and isolation on bird community attributes, changes in vegetation across fragments were analysed and summarised using principal components analysis. There were pronounced differences between fragments in their vegetation attributes. Tree density, for instance, varied nearly four-fold from a low of 196 trees/ha in Korangumudi to a high of 755 trees/ha in Karian Shola (Table 6.5). Although basal area varied in a similar manner across sites, these variables did not show a clear trend in relation to fragment area. Nevertheless, although some small and disturbed fragments had high tree densities and basal areas comparable to those of large fragments, this was contributed to a significant extent by pioneer trees such as *Macaranga indica* and exotic species such as *Maesopsis emeni*. Other parameters such as average canopy cover, canopy height, vertical stratification, and shrub density, were lower in disturbed small fragments and one medium-sized fragment (Korangumudi), than in less-disturbed fragments of any size. Horizontal heterogeneity showed an opposite trend (Table 6.5).

Principal components analysis selected and combined correlated vegetation variables and identified two uncorrelated factors that summarised the trends of change in vegetation, explaining 71% of the total variation. The first factor (PC1) explained 44% of the variation in the data, and the second (PC2) explained a further 27%. PC1 was positively correlated to canopy cover, canopy height, vertical stratification, and shrub density, and negatively with horizontal heterogeneity (Table 6.6). PC2 was positively correlated to tree density, basal area, and leaf litter depth (Table 6.6). The PC1 site scores can be taken to represent their habitat structure (vertical and horizontal), while the PC2 scores index their woody biomass. The ordination of sites in PC1-PC2 space indicates the major trends of change in habitat structure and woody biomass across sites (Figure 6.6). The (Euclidean) distance between any two sites in this ordination is a measure of their difference in vegetation characteristics.

Table 6.5: Changes in vegetation attributes across the rainforest fragments in the Anamalai hills.

Para-meter[a]	Fragment[b]												
	K2	K1	V4	V3	PA	TF	K0	PU	AN	MA	KS	VA	IYAK
CCOV	86.5	79.6	78.1	96.3	92.5	96.3	68.2	89.0	96.2	95.0	98.2	94.7	97.7
	(4.19)	(3.75)	(2.6)	(0.87)	(0.79)	(1.24)	(3.17)	(1.26)	(0.65)	(1.44)	(0.16)	(0.72)	(0.54)
CHT	17.8	19.3	17.8	17.4	22.4	31.3	20.7	22.7	22.7	24.5	27.0	28.6	22.7
	(0.95)	(1.57)	(2.19)	(2.22)	(1.75)	(1.93)	(2.09)	(1.87)	(1.83)	(1.11)	(0.72)	(1.41)	(1.39)
SDEN	6.6	10.0	6.7	12.8	34.2	11.0	11.5	7.9	26.3	11.6	23.8	15.8	10.2
	(0.72)	(1.02)	(0.58)	(0.75)	(2.97)	(0.92)	(2.89)	(0.78)	(3.00)	(1.08)	(2.42)	(1.67)	(0.64)
VSTR	4.3	3.7	4.3	4.64	5.6	5.32	3.36	5.12	4.84	5.08	5.12	5.44	4.97
	(0.42)	(0.33)	(0.39)	(0.27)	(0.24)	(0.24)	(0.19)	(0.21)	(0.24)	(0.29)	(0.25)	(0.21)	(0.28)
HHET	9.84	9.05	9.2	5.82	4.37	4.44	5.67	4.12	4.87	5.67	4.83	3.84	5.59
TDEN	424	382	484	295	534	331	196	239	431	582	755	446	697
	(40.3)	(12.0)	(39.4)	(7.6)	(13.7)	(5.6)	(1.9)	(2.4)	(4.4)	(5.8)	(7.6)	-	(5.00)
BASA	141.2	62.9	50.7	33.5	47.5	40.3	31.3	52.5	84.5	114.4	95.9	36.3	74.4
LITT	5.2	5.2	3.1	4.0	4.3	4.8	2.9	3.6	5.1	6.6	3.7	3.6	6.9
	(0.79)	(0.35)	(0.34)	(0.21)	(1.29)	(0.45)	(0.24)	(0.39)	(0.50)	(0.61)	(0.30)	(0.30)	(0.45)

[a]—CCOV = canopy cover (%), CHT = canopy height (m), SDEN = shrub density (number of shrubs/plot), VSTR = vertical stratification (number of vertical strata), HHET = horizontal heterogeneity (%CV of VSTR), TDEN = tree density (trees/ha), BASA = basal area (m²/ha), LITT = leaf litter depth (cm).

[b]—Fragment codes as in Table 6.1

Table 6.6: Results of principal components analysis of vegetation variables showing eigenvalues and Pearson's correlations between original variables and extracted components.

Component	PC1	PC2
Eigenvalue	3.523	2.158
Variation explained (%)	44.0	27.0
Cumulative %	44.0	71.0
Pearson' correlations (*df* = 11)		
Canopy cover	0.79***	0.44
Canopy height	0.79***	–0.06
Shrub density	0.63*	–0.02
Vertical stratification	0.90***	0.18
Horizontal heterogeneity	–0.87***	0.33
Tree density	0.38	0.72*
Basal area	–0.16	0.87**
Leaf litter depth	0.11	0.81**

*—$P < 0.05$, **—$P < 0.01$, ***—$P < 0.001$ (*df* = 11)

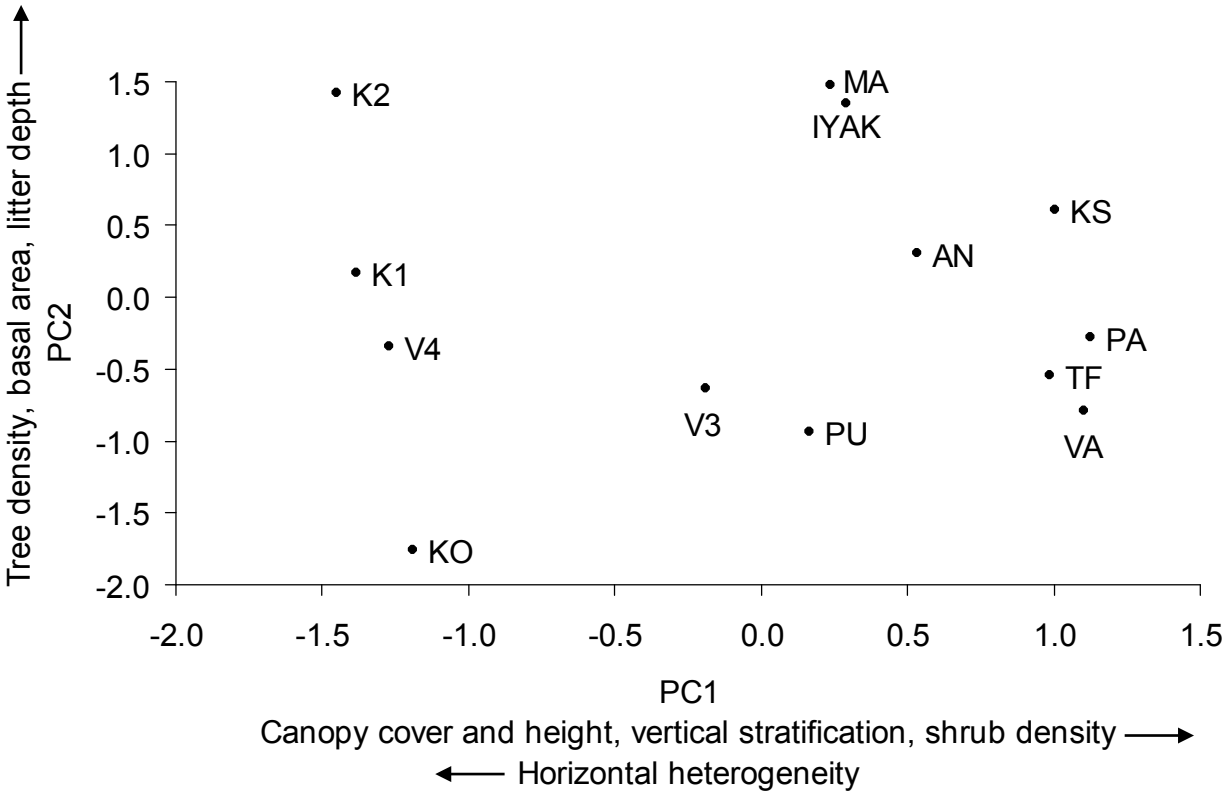

Figure 6.6: Ordination of rainforest fragments in the Anamalai hills using principal components analysis of vegetation variables.

6.4.1.4 *Influence of area, isolation, habitat structure, and altitude*

The influence of fragment area and isolation, on bird species richness and abundance was assessed through stepwise multiple regression analyses. Isolation was measured as the distance of each site from the largest 'control' fragment (IYAK), which itself was considered to be non-isolated (isolation = 0 km). Habitat structure was indexed by the PC1 and PC2 scores of the fragments. Table 6.7 indicates significant predictor variables, excluding altitude, which although included in the analyses was not found to be a significant predictor of any of the bird community variables.

The variables influencing total and resident bird species richness were similar. Bird species richness (all species) increased significantly with fragment area. In addition, it tended to decline with increasing PC2 scores (woody biomass), although this was not statistically significant ($P \leq 0.15$, Table 6.7). The species richness of open-country birds was unrelated to fragment area. Instead, it was strongly negatively influenced by both PC1 (habitat structural development) and PC2, and showed a tendency to be positively related to isolation from the largest fragment. In contrast, rainforest bird species richness, increased significantly with fragment area, and tended to also increase with the structural development of rainforest vegetation (PC1, Table 6.7).

The predictor variables influenced point richness and abundance somewhat differently. The richness and abundance with all species included was not significantly related to any variable, as may

be expected, because, these parameters were nearly constant across sites (Figures 6.3a, 6.4a). The point richness and abundance of open-country birds decreased significantly with forest structural development (PC1) and also tended to decrease with fragment area. In contrast, point richness and abundance of rainforest birds was strongly related positively only to rainforest structural development (PC1, Table 6.7). Thus, although fragment area more strongly influenced fragment-level richness of rainforest birds, the structural development of rainforest vegetation had greater influence on point richness and abundance of rainforest birds. The abundance of rainforest birds also showed a tendency to be higher in fragments that were closer to the Iyerpadi-Akkamalai 'control' site (Table 6.7).

Table 6.7: Results of stepwise multiple regression of bird species richness and abundance measures on area, altitude, and habitat structure of fragments in the Anamalai hills.

Dependent variable	Beta (standardized regression coefficient)					Regression ANOVA		
	LogArea	PC1	PC2	Isolation	R^2	*F*	*df*	*P*
Total species richness								
All	0.727**	–	–0.360$^+$	–	0.586	7.09	2,10	0.0121
Open-country	–	-0.688*	-0.549*	0.580$^+$	0.731	5.45	4,8	0.0204
Rainforest	0.603*	0.360$^+$	–	–	0.791	18.94	2,10	0.0058
Resident species richness								
All	0.775**	–	–0.336$^+$	–	0.642	8.96	2,10	0.0059
Open-country	–	-0.706*	-0.504*	0.655$^+$	0.714	5.00	4,8	0.0256
Rainforest	0.605**	0.380$^+$	–	–	0.825	23.62	2,10	0.0002
Species richness/point								
All	–	–	–	–	–	–	–	–
Open-country	–0.357$^+$	–0.621**	–	–	0.817	22.38	2,10	0.0002
Rainforest	–	0.806***	–	–	0.650	20.41	1,11	0.0009
Abundance/point								
All	–	–	–	–	–	–	–	–
Open-country	–0.364$^+$	–0.542*	–	–	0.697	11.51	2,10	0.0026
Rainforest	–	0.784**	-	-0.361$^+$	0.543	5.95	2,10	0.0198

Altitude of fragments was included as a variable in the analyses but is not listed above as only significant results are presented; $^+ - P \leq 0.15$, * $- P \leq 0.05$, ** $- P \leq 0.01$, *** $- P \leq 0.001$.

6.4.2 Changes in bird species composition

6.4.2.1 *Patterns of species turnover*

The similarity in bird species composition between sites was calculated with the Morisita index using the data on bird densities in each fragment. The matrix of similarities was used as input for nonmetric multidimensional scaling which converged on a two-dimensional configuration (stress = 0.073). Ordination of fragments on these two dimensions (Figure 6.7) graphically represents the relative

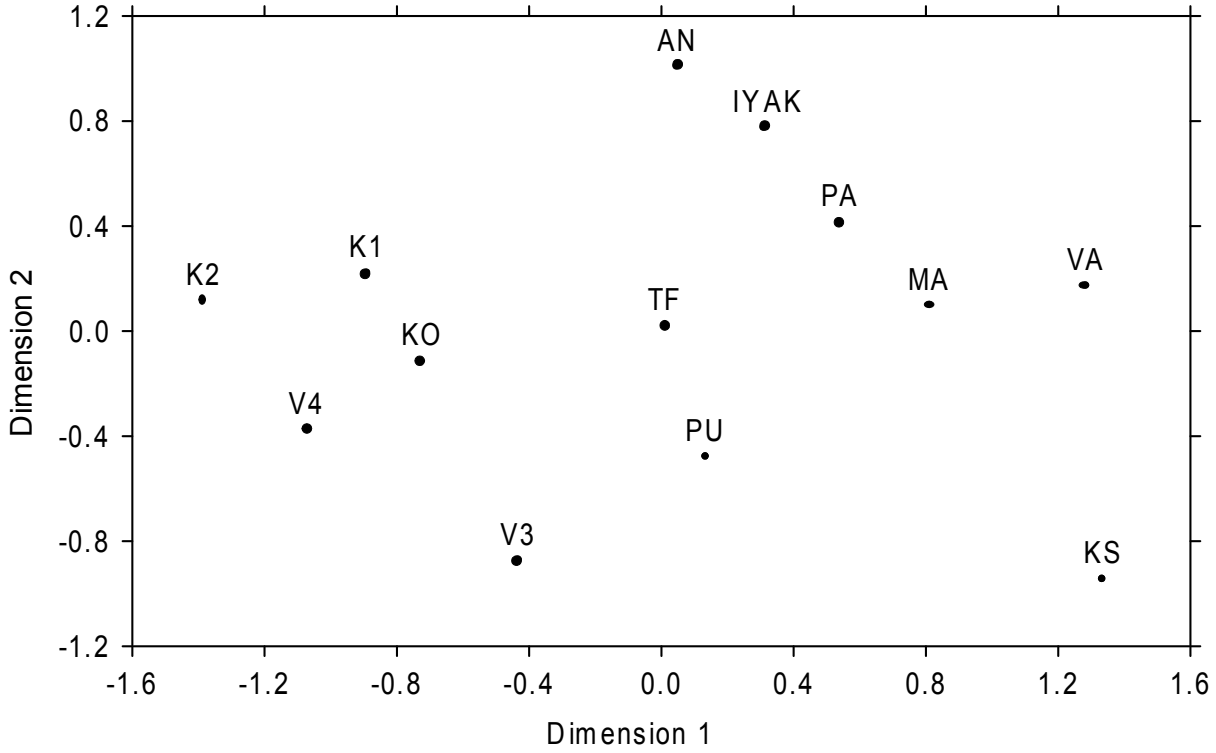

Figure 6.7: Similarity in bird community composition among rainforest fragments in the Anamalai hills illsutrated using multidimensional scaling ordination.

similarities between sites—the greater the distance between any two sites in the figure, the more different their bird community composition.

The ordination shows that three of the smallest fragments (K2, K1, V4) and one highly disturbed medium-sized fragment (KO) are similar in bird species composition as indicated by their proximity (Figure 6.7). All the large fragments (IYAK, VA, MA, AN), and one of the relatively undisturbed small fragments (PA), form another group towards the top right, with three medium-sized fragments (PU, TF, V3) occupying intermediate positions. One of the large fragments (KS) appeared to be relatively dissimilar from all other fragments in the bird community composition.

The similarity in bird species composition of sites with the control site (IYAK) was not significantly related to the fragment area ($\tau = 0.212$, $N = 12$, $P = 0.337$; Figure 6.8a). The analysis was repeated excluding three low-elevation sites, which tended to differ in bird community composition (open circles in Figure 6.8a). Bird community similarity with the control site showed a stronger positive trend indicating that larger fragments tended to be more similar to the control site, but this was not statistically significant ($\tau = 0.444$, $N = 9$, $P = 0.095$). This weak relationship was due to the wide variation in intermediate-sized fragments. Particularly notable was the large difference (>50%) between the highly disturbed V3 and relatively undisturbed PA, in their bird community similarity with IYAK despite differing only 3 ha in area (Figure 6.8a). After the large fragment Andiparai (AN), Pannimade (PA) was the most similar site in bird community composition to the control site.

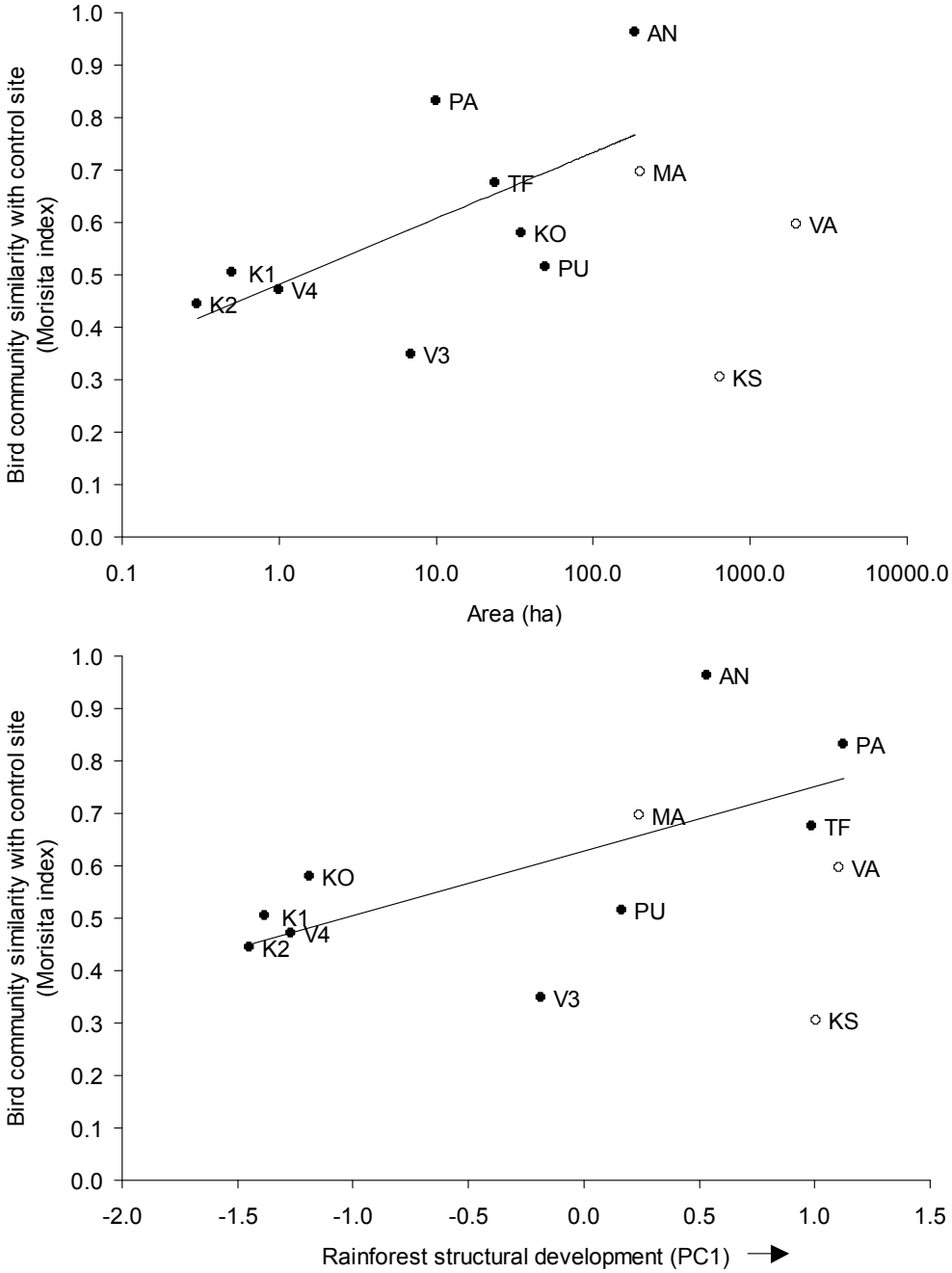

Figure 6.8: Similarity of rainforest fragments with the control site (Iyerpadi-Akkamalai) in bird community composition in relation to fragment area (a, upper panel) and rainforest habitat structure indexed by PC1 (b, lower panel). Lower elevation sites are indicated by open circles.

Besides area, the influence of isolation, PC1, PC2, and altitude on the similarity in species composition with IYAK were examined using Kendall correlations. Only forest structural development (PC1) showed a positive correlation (all sites: $\tau = 0.364$, $P = 0.0998$; exluding low-elevation sites: $\tau = 0.556$, $P = 0.0371$; Figure 6.8b). Thus, similarity in habitat structure with the control site appeared to exert a stronger influence on the similarity in bird community composition.

6.4.2.2 *Influence of site and habitat attributes on species composition and turnover*

Sites may be expected to be less similar in bird species composition if they were geographically or altitudinally distant, or if they were dissimilar in habitat structure or tree species composition. This was examined in two ways using stepwise multiple regression models. First, the similarity of each of the 12 fragments with the control (IYAK) fragment was related to their corresponding physical distances or dissimilarities in habitat with IYAK. Second, a similar approach was used using the data from the matrix of similarities between all possible pairs of sites (N = 78 pairs). In both cases, the analyses were carried out separately for bird community similarities calculated with the sets of (a) all species, (b) open-country species, and (c) rainforest species (Table 6.8).

Similarity of fragments with the control site in bird community composition (all species or only rainforest species) was related to two main factors—tree species composition and area. Fragments that were more dissimilar in tree species composition or were more different in area had less similar bird community composition, with the effects of variation in tree species composition being stronger than the effects of area (Table 6.8). In contrast, the similarity in community composition considering open-country species alone was negatively related to altitudinal distance and positively to geographic distance from the control site (Table 6.8).

Table 6.8: Results of stepwise multiple regression exploring the effects of differences between fragments in location and habitat attributes on their similarity in bird community composition in the Anamalai hills.

	Beta (standardized regression coefficient)					Regression ANOVA			
	AREA DIFF	TREE DISM	STRU DISM	GEOG DIST	ALTI DIST	R^2	F	df	P
Similarity with control site (IYAK)									
Species set									
All	-0.803*	-0.908*	0.336	-	-0.293	0.755	5.40	4, 7	0.0264
Open-country	-	-	0.202	0.671*	-1.262**	0.773	9.10	3, 8	0.0059
Rainforest	-0.685*	-0.936*	0.477^{+}	-	-0.327	0.753	5.34	4, 7	0.0271
Similarity between sites (all possible pairs)									
Species set									
All	-0.256**	-0.263*	-0.247*	-0.251*	-	0.438	14.25	4, 73	< 0.0001
Open-country	-	-0.212^{+}	-0.248*	0.382*	-0.534***	0.269	6.73	4, 73	< 0.0001
Rainforest	-0.182^{+}	-0.281*	-0.162^{+}	-0.276*	-	0.382	11.26	4, 73	< 0.0001

Indices of distance/dissimilarity between fragments:
AREA DIFF—difference in the logarithms of the area of the fragments
TREE DISM—dissimilarity in tree species composition (1-Morisita index)
STRU DISM—structural dissimilarity (Euclidean distance using PC scores)
GEOG DIST—geographic distance between sites (km)
ALTI DIST—difference in average altitudes of the sites (m)
Significant coefficients are marked: $^{+}-P \leq 0.15$, $*-P \leq 0.05$, $**-P \leq 0.01$, $***-P \leq 0.001$.

These results were reinforced by the analysis using data on all possible pairs, but in addition, other variables were also found to be influential. Bird community similarity (all species and rainforest species only) was negatively related to structural dissimilarity and geographic distance, in addition to difference in area and dissimilarity in tree species composition as in the first analysis. The bird community composition considering open-country species alone was found to be negatively related to structural dissimilarity between sites, besides the relationships with physical distance measures described above (Table 6.8). It must be noted, however, that this analysis was done with 78 cases (measures of similarity/distance) for each variable, derived by all possible pairs comparisons of only 13 sites. The resultant *P*-values of statistical significance must be treated with caution. The low R^2 (< 0.44) also indicates that considerable variation remained unexplained even after accounting for the effects of these multiple factors.

6.4.2.3 *Nested subset analyses*

Nested subset structure of community composition, analysed with the program NESTCALC, showed distinct patterns for each species set analysed. For all three species sets (all, open-country, or rainforest birds) the bird community was found to be highly significantly nested (Table 6.9). The nestedness is assessed here, however, by arranging sites in the order of maximal matrix packing—which mostly corresponds to what would be obtained by ordering the sites on the basis of bird species richness. Depending on the species set considered, the rank ordering of sites varies and is also different from the rank-ordering based on fragment area (Table 6.9). For instance, although Andiparai

Table 6.9: Rank-order of rainforest fragments in the Anamalai hills on the basis of area and following nested subset analysis for each species set.

Rank	Fragment area	Species set (species richness)		
		All	Open-country	Rainforest
1.	IYAK	KO (63)	KO (21)	IYAK (51)
2.	VA	KS (56)	V3 (13)	MA (49)
3.	KS	PU (55)	K2 (12)	KS (48)
4.	MA	IYAK (54)	PU (11)	VA (47)
5.	AN	VA (52)	K1 (9)	PU (44)
6.	PU	TF (48)	KS (8)	TF (42)
7.	KO	PA (50)	PA (8)	PA (42)
8.	TF	MA (53)	V4 (8)	KO (42)
9.	PA	V3 (50)	VA (5)	V3 (37)
10.	V3	AN (42)	TF (6)	AN (38)
11.	V4	K2 (31)	MA (4)	K1 (21)
12.	K1	K1 (29)	AN (4)	K2 (19)
13.	K2	V4 (22)	IYAK (3)	V4 (14)
	Nestedness statistics			
	Matrix fill (%)	42.2	27.7	49.2
	Matrix temperature (T°)			
	Observed	32.05	14.03	24.61
	Expected (SD)	64.55 (3.01)	53.15 (6.08)	63.05
	$P(T<\text{observed})$	5.64×10^{-27}	6.80×10^{-11}	6.64×10^{-32}

Fragment codes as in Table 6.1.

(AN) is ranked 5 according to area, it ranks 10 in the gradient of nestedness of rainforest bird species. In contrast, the small fragment Pannimade (PA) ranked 9 on area, climbs to greater importance at rank 7 when rainforest bird species richness and nestedness are considered.

The pattern of nestedness across fragments is illustrated in Figure 6.9. The filled squares indicate occurrences, the empty one absences. The line is an estimate of an extinction threshold and populations (squares) below the line or close to it may be expected to be the first to disappear if species richness (or area) of the fragment declines further. Despite the nestedness being highly significant, it is clear that there is considerable scatter about the line and many idiosyncratic species occurring in sites where they are not expected under the condition of perfect nestedness. Similarly there are idiosyncratic sites showing unexpected presences or absences of species (Figure 6.9). The nestedness is thus far from perfect and other factors may be at work.

6.4.3 Plantations and landscape matrix effects

6.4.3.1 *Species richness and composition in plantations*

The data from the tea, coffee, and *Eucalyptus* plantations (25 point counts in each) were compared with an equal sample of 25 point counts selected at random from the samples taken in the rainforest control site at a similar elevation (Iyerpadi portion). In total, 78 bird species were recorded in the plantations. Of these, 38 bird species were seen only in one of the plantation types (mostly in coffee) and were not recorded in the rainforest sample. This included 14 rainforest bird species and 24 open-country species. These 14 rainforest bird species included 8 species typically found in rainforests at lower elevations than Iyerpadi (below 1,100 m), 5 species seen infrequently in rainforest interior and more along edges on other occasions (Grey Junglefowl, Grey Wagtail, Eurasian Blackbird, Rufous Babbler, Emerald Dove), and one vagrant represented by a single detection in *Eucalyptus* plantation (Ashy Drongo). Seventeen bird species were seen only in the rainforest site and were not recorded from plantations. All 17 species were rainforest birds and included species such as the Dark-fronted Babbler, Malabar Trogon, Great Hornbill, Greater Flameback, Brown-cheeked Fulvetta, Yellow-browed Bulbul, and all three endemic flycatchers: Black-and-Orange Flycatcher, Nilgiri Flycatcher, and White-bellied Blue Flycatcher.

The total numbers of bird species recorded in tea, *Eucalyptus*, and coffee plantations and in rainforest were: 26, 41, 50, and 40, respectively. The corresponding numbers of rainforest bird species recorded across these four strata were: 10, 21, 30, and 37, respectively. The tea plantation was clearly the poorest habitat for rainforest birds, whereas the coffee plantation had only slightly lower bird species richness than rainforests (Figure 6.10).

These patterns were also clear in the analyses of point richness and abundance data. Bird species richness per point count was highly significantly different across the four strata, irrespective of species set considered—all, open-country, or rainforest birds (Kruskal-Wallis analysis of variance,

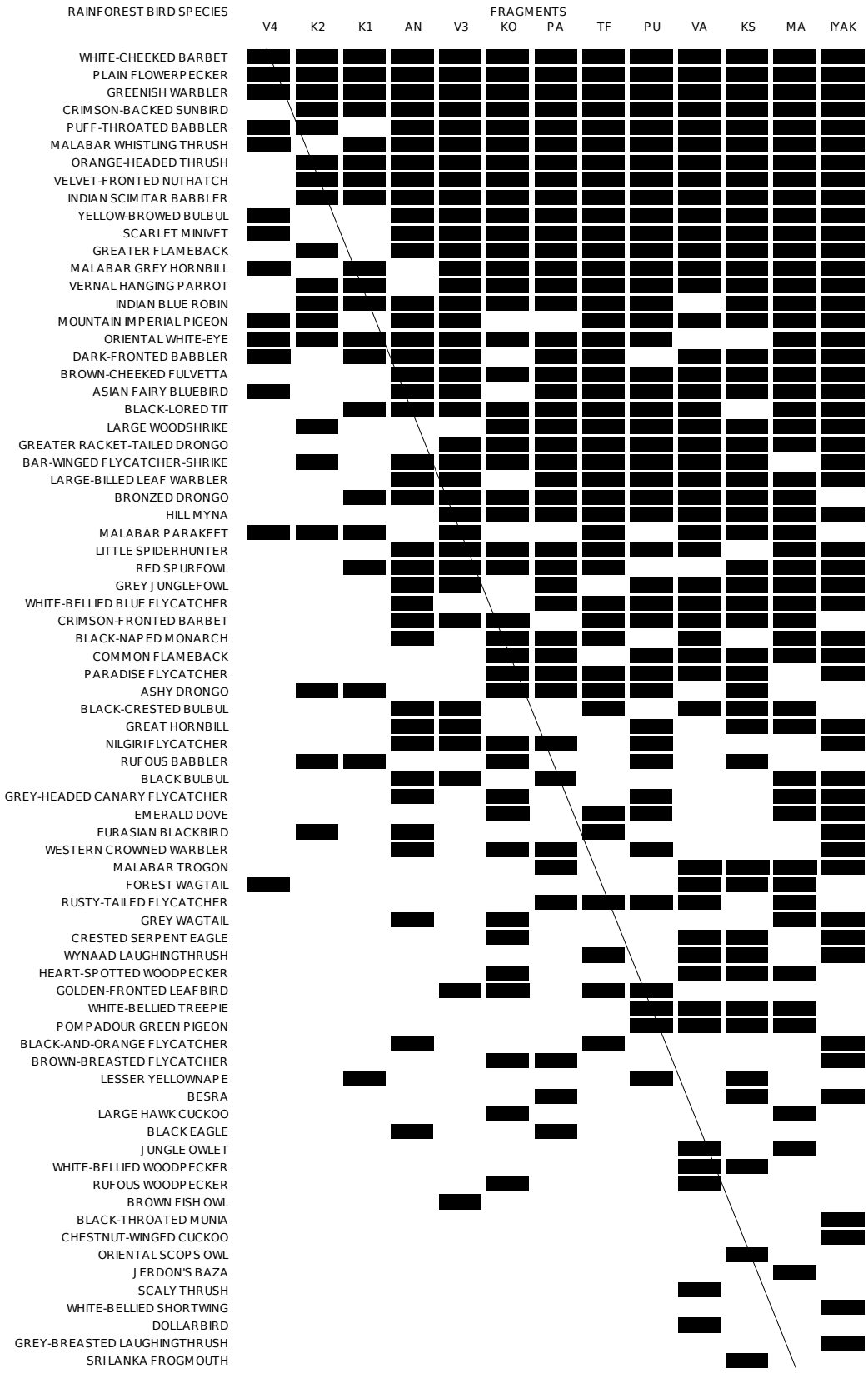

Figure 6.9: Nested distributions of rainforest bird species across fragments: results of nested subsets analyses using the program NESTCALC. The line can be taken to indicate an extinction threshold determined from the data. Each black bar represents the occurrence of a species (row) in the corresponding fragment (column).

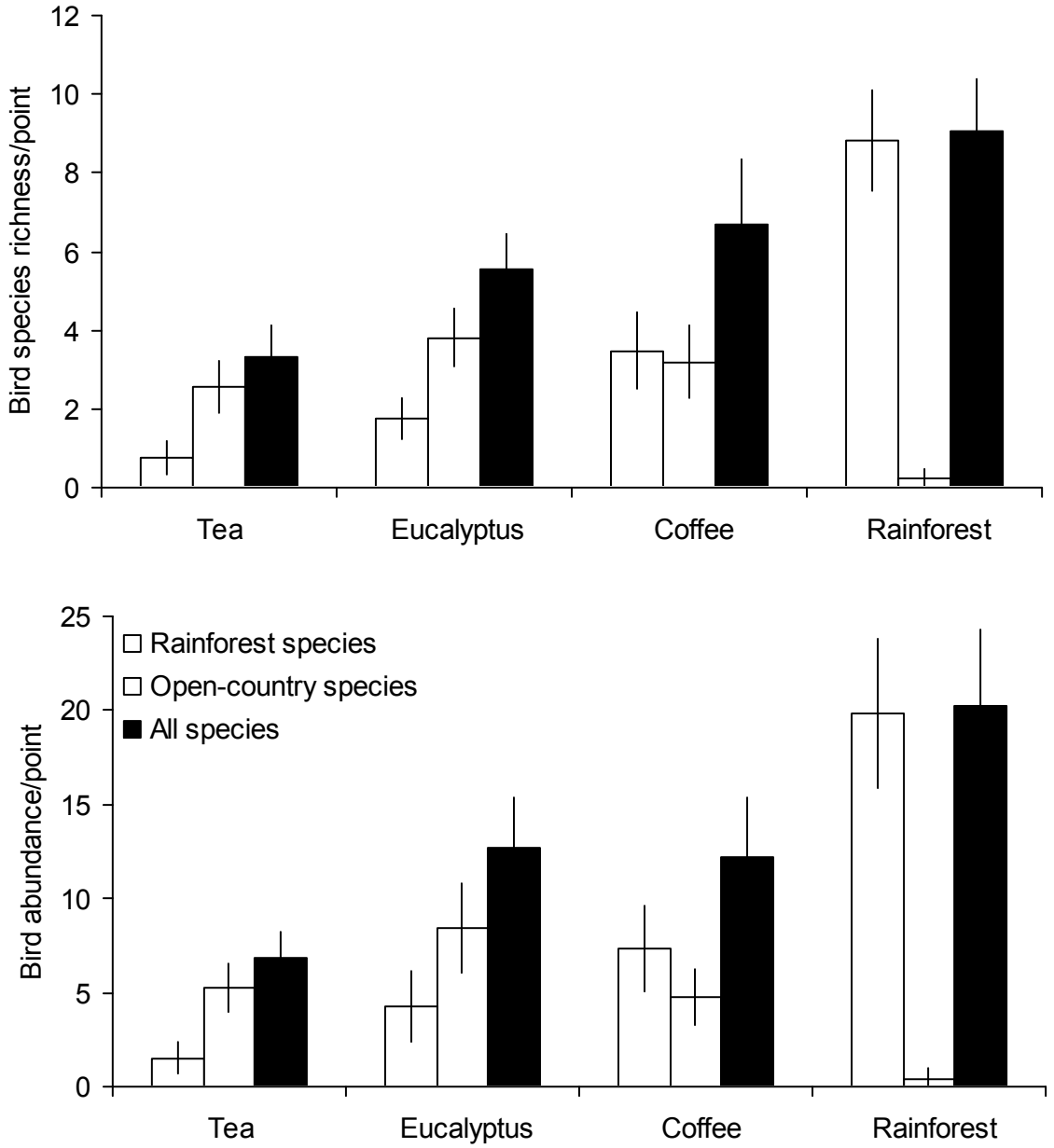

Figure 6.10: Bird species richness (a, upper panel) and bird abundance measured as number of individuals (b, lower panel) in the three plantation types and the control primary rainforest site in the Anamalai hills. Bars indicate average per point count sample with errors bars indicating ± 1 SE.

$H > 34.9$, $P < 0.0001$). The average richness and 95% confidence interval for each strata are presented in Figure 6.10a. Total and rainforest bird species richness per point increased significantly from tea to *Eucalyptus* and coffee plantations and to rainforest. Open-country bird species richness was significantly lower in rainforest and roughly the same in all plantation types. Bird abundance per point also showed a similar pattern (Figure 6.10b). Rainforest bird abundance was over ten times higher in rainforest than in tea plantation, and over twice the abundance in coffee plantation.

6.4.3.2 *Effects of matrix on species survival in fragments*

The relative tolerance of rainforest bird species to the matrix of plantations was classified into three categories: matrix intolerant (17 species that occurred in the rainforest but were absent from the plantations), intermediate tolerance (species that used both the matrix and rainforest), high tolerance (species that appeared to be confined to plantations but were actually only encountered more frequently in plantations). Two main questions were addressed. First, did bird species that differed in their matrix tolerance also differ in the average densities they attained in small and medium-sized rainforest fragments? Second, was matrix tolerance related to species persistence in small and medium-sized fragments? Persistence was measured by a simple index: the ratio of average density in small (or medium-sized) fragments to average density in large fragments. Persistence index (PI) values > 1 indicated species whose population densities were higher in the smaller fragments, whereas index values < 1 indicated species that declined and 0 indicated species that disappeared in the fragments of the smaller size class.

The results in Table 6.10 illustrate the influence of matrix tolerance on species persistence in fragments. Species density varied significantly across tolerance categories: the species classified as intermediate in matrix tolerance occurred in all fragment size classes at higher densities than species

Table 6.10: Density and persistence of rainforest birds in different-sized fragments in relation to their tolerance of the landscape matrix of plantations in the Anamalai hills.

Parameter	Matrix tolerance[a]			Kruskal-Wallis ANOVA	
	Intolerant *N* = 17	Intermediate *N* = 20	High *N* = 14	*H*	*P*
Density in individuals/ha (SE)					
In small fragments	0.11 (0.04)	0.50 (0.13)	0.18 (0.08)	12.17	0.0023
In medium-sized fragments	0.29 (0.10)	0.68 (0.12)	0.17 (0.05)	14.12	0.0009
In large fragments	0.49 (0.16)	0.58 (0.10)	0.16 (0.05)	13.47	0.0012
Persistence[b] (SE)					
In small fragments	0.47 (0.22)	0.86 (0.13)	6.08 (2.81)	7.26	0.0265
In medium-sized fragments	0.98 (0.31)	1.28 (0.14)	10.67 (6.87)	5.57	0.0618

[a]—Intolerant = avoids matrix, Intermediate = uses matrix and rainforest, High = more frequent in matrix; *N* = number of bird species in each tolerance category.
[b]—Persistence was estimated for each species as the ratio of average density in that fragment class to the average density in large fragments.
Tabled values are means and SE calculated across the *N* species in each tolerance category.

of low tolerance. Surprisingly, species of high matrix tolerance also attained low densities (Table 6.10) in fragments of all size classes. This must be weighed against the fact that many of these species would have been rarer or absent as they were rainforest birds of lower-elevations. The densities of species in smaller fragments must be viewed relative to densities attained in the large fragments and this is done by the persistence index.

Analysis of species persistence indicated clearly an increase in persistence in relation to increasing tolerance of matrix, particularly in the bird community of small fragments (Table 6.10). Thus species that are highly tolerant of the matrix occur at much higher densities in small fragments than in the large fragments (average PI = 6.08). Species of intermediate tolerance occur at only slightly lower densities (average PI = 0.86) than in large fragments, whereas densities of matrix-intolerant species are much lower (average PI = 0.47). In medium-sized fragments, even matrix-intolerant species appear to persist, while more tolerant species increase substantially in abundance. The species of birds that occur in fragments and their abundances are thus linked to their tolerance of human-altered habitats such as plantations in the surrounding landscape.

6.4.4 Responses of diet-guilds and species categories

6.4.4.1 *Diet-guilds*

The number of bird species in different diet-guilds showed two main trends in relation to fragmentation. Bark-surface feeders, carnivores, omnivores, frugivores, understorey and terrestrial insectivores appeared to increase in species richness with fragment area. Nectarivore and canopy insectivore species richness were not directly related to fragment area, tending to be higher in medium-sized fragments (Table 6.11).

Regression analyses showed that bark-surface feeder, frugivore, and terrestrial insectivore species richness increased primarily in response to increasing fragment area (Table 6.11). Carnivores also responded mainly to fragment area—the significant positive relation with isolation in Table 6.11 is due to more species being recorded from the fragments at lower elevations (PA, MA, KS, and VA) that were also the most distant ones from the IYAK control site. Low-elevation sites also had more species of omnivores as indicated by the significant negative regression coefficient in Table 6.11. Nectarivores showed no significant relationship with measured parameters. The only guilds that showed strong relationships with habitat measures were the canopy and understorey insectivores. Species richness of both these guilds was positively associated with PC1, indicating that fragments with better forest structural development and higher shrub density tended to contain more species in these guilds (Table 6.11).

Within each guild, species showed a diversity of responses ranging from being nearly ubiquitous to being confined to large fragments or those that contained well-developed habitat structure (Appendix 4). Bark-surface feeders, carnivores, omnivores, frugivores, and understorey

Table 6.11: Species richness of diet-guilds and different bird species categories in relation to area, habitat, altitude, and isolation of rainforest fragments in the Anamalai hills—results of stepwise multiple regression analyses.

	Beta (standardidised regression coefficient)					Regression ANOVA				Kendall
	Log(area)	PC1	PC2	Altitude	Isolation	R^2	F	df	P	correlation[a]
Diet-guild										
Bark-surface feeder	0.659**	-	-	-	0.359$^+$	0.859	16.32	3,8	0.0009	0.641**
Omnivore	-	-	-	-0.427$^+$	-	0.712	6.60	3,8	0.0148	0.586**
Carnivore	0.424$^+$	-	-	-	0.785*	0.811	11.44	3,8	0.0029	0.642**
Frugivore	0.788**	-	-	-	-	0.620	16.35	1,10	0.0024	0.541**
Nectarivore	-	-	-	-	-	-	-	-	-	0.014
Canopy insectivore	-	0.534*	-0.475$^+$	-	-	0.531	5.10	2,9	0.0331	0.259
Understorey insectivore	0.440$^+$	0.632*	-	0.286$^+$	-	0.849	15.02	3,8	0.0012	0.568**
Terrestrial insectivore	0.624$^+$	-	-	-	-	0.295	1.89	2,9	0.2068	0.403$^+$
Species category										
All migrants	-	-	-	-	-	-	-	-	-	0.235
Open-country migrants	-	-0.565*	-0.646**	-	-	0.709	10.95	2,9	0.0039	-0.424*
Rainforest migrants	-	-	-	-	-	-	-	-	-	0.390$^+$
Endemic species	0.475$^+$	-	-	-	-	0.628	7.60	2,9	0.0117	0.688***
Priority species	0.585*	0.277$^+$	-	-0.251$^+$	-	0.907	25.87	3,8	0.0002	0.658**

[a]—Kendall rank-order correlation coeeficients with log(area) of fragment
$^+$—$P < 0.15$, *—$P < 0.05$, **—$P < 0.01$, ***—$P < 0.001$ (N = 13 fragments)

insectivores were all represented by fewer than three species in the three smallest fragments (up to 1 ha in area) and more species in larger fragments.

6.4.4.2 *Migrants, endemics, and priority species*

The number of species of migrants, Western Ghats endemics, and priority (rare, restricted-range, discontinuously distributed, and threatened) species were also analysed in relation to fragment area, isolation, altitude, and habitat. Among migrants, no trends were evident when all species or rainforest species were considered. The number of species of open-country migrants was negatively related to both PC1 and PC2 and also showed a trend of decrease with fragment area (Table 6.11). A noteworthy pattern is that both the number of endemic species and number of priority species was mainly related to fragment area. Priority species richness was also weakly positively associated with forest structural development (PC1) and tended to decline with increasing elevation (Table 6.11).

Within each category also species showed a diversity of responses. Among the 11 endemic species recorded during the study, five (Malabar Parakeet, Malabar Grey Hornbill, Nilgiri Flycatcher, Rufous Babbler, Crimson-backed Sunbird) were seen in fragments less than 10 ha in area. Medium-sized (10-100 ha) fragments contained these five plus an additional four species (Black-and-Orange Flycatcher, White-bellied Treepie, White-bellied Blue Flycatcher, Wynaad Laughingthrush). Only two species appeared to be restricted to the largest fragments (Grey-breasted Laughingthrush, White-

bellied Shortwing), both being high-altitude forms seen in the Akkamalai portion of the control site and unlikely to occur in the lower elevation fragments. Both these species may occur in smaller fragments at higher elevations. Among the 24 priority rainforest bird species, only six were confined to large fragments (Dollarbird, Sri Lanka Frogmouth, White-bellied Woodpecker, Jerdon's Baza, Black-throated Munia, Scaly Thrush, the first three being low-elevation species). Eight species were widespread from the smallest to the largest fragments, and ten species occurred in medium and large fragments. It must be noted that species distributions may not have been related merely to fragment area. For instance, the Malabar Trogon, was found in all large fragments, but occurred in the 10 ha Pannimade fragment in which the habitat was relatively undisturbed.

6.5 DISCUSSION

The major effects of fragmentation on bird communities in this study are clear. Trends in bird species richness were related to fragment area and habitat and were not predicted by the null model of passive sampling. With increasing area of the fragment, the species richness of rainforest birds increases log-linearly. Besides area, the structural development of rainforest vegetation (PC1) had positive effects on rainforest birds (increasing richness and similarity with the control site) and negative effects on open-country species. Bird community composition was also correlated with site and habitat features and showed a nested subset structure, indicating possible differential extinction of species in relation to fragmentation. Plantations, particularly tea and *Eucalyptus* and to a lesser extent coffee, had deleterious effects on a large number of rainforest bird species, although birds that tolerated or thrived in plantations were able to persist in small and medium-sized fragments also, and often at higher densities. Diet-guilds and species categories showed varying responses to fragmentation, with endemics, priority species, and diet-guilds such as carnivores, frugivores, bark-surface feeders, and understorey insectivores appearing to be particularly susceptible. The diversity of responses across species indicates that the observed effects are a consequence of various underlying factors and mechanisms.

6.5.1 Biological infiltration

A primary consequence of rainforest fragmentation and conversion to plantations in the Valparai landscape has been the influx of at least 25 species of open-country birds (21.3% of species recorded in the study). These non-rainforest birds include species such as Ashy Prinia, Common Tailorbird, Red-whiskered Bulbul, Golden Oriole, Grey-headed Myna, Asian Brown Flycatcher, Magpie Robin, and Chestnut-tailed Starling that are typically found in tropical dry thorn and dry deciduous forests in the adjoining areas of the Anamalai hills as well as over most of the Indian sub-continent (Ali and Ripley 1983, Daniels 1997). These species have successfully colonised and utilise the small and medium-sized fragments, particularly highly disturbed sites such as Korangumudi, in which a number

of rainforest bird species appear to be locally extinct. The replacement of rainforest birds typical to a region by widespread species of open-country following human-caused habitat alteration has also been noted in earlier studies (Leck 1979, Daniels *et al.* 1990a, 1992, Raman *et al.* 1998, Raman 2001).

It has been widely recognised that non-forest and second-growth species may occur at the periphery of fragments due to *edge effects*, particularly within 100 m from the periphery of fragments (Lovejoy *et al.* 1986, Wiens 1989, Malcolm 1994, Murcia 1995, Restrepo and Gomez 1998). In the present study, open-country birds not only occurred along fragment edges, but were regularly seen in the interior of medium-sized fragments, even over 100 m from the edge. This is mainly attributable to the habitat disturbance (particularly tree cutting for fuelwood and timber) that opened up the canopy and understorey all across the fragment. The consequent structural changes as well as growth of deciduous and pioneer tree species (e.g., *Macaranga peltata*) increase the resemblance of these fragments to more open deciduous forests while decreasing their similarity with undisturbed primary rainforest. This then enables open-country species to colonise even the interior of fragments and not merely the edges. This process of influx of non-forest species replacing forest species in local communities can be termed *biological infiltration* as the colonising species are often found in the interior of fragments. This phenomenon is not a result of fragmentation *per se* because small and isolated fragments such as Pannimade that were less disturbed had fewer (8) open-country species than highly disturbed fragments of similar size (V3, 13 species) or larger (KO, 21 species). Biological infiltration as seen here is also distinct from biological invasions, which typically involve the proliferation of a few, mostly weedy, often exotic, species. Infiltration, in contrast, involves species native to regional habitats establishing in atypical habitats, at large or sparse population sizes. Such a process has been noted in studies ranging from beetles in fragmented temperate deciduous forests (As 1999), butterflies in Amazonia (Brown and Hutchings 1997), and reptiles (Ishwar 2001) and small carnivorous mammals (Mudappa 2001) in the fragments of the Anamalai hills.

The infiltration of species is a matter of conservation concern as widespread species of drier forests benefit at the cost of more restricted, often rare, rainforest species, whose conservation is of higher priority (Usher 1986). The cessation or reversal of rainforest habitat alteration that creates more openings is required through protection or restoration for the maintenance of rainforest bird community structure.

6.5.2 Bird species richness: area *versus* habitat effects

The above process of biological infiltration of open-country birds into rainforest areas leads to the pattern of higher overall bird species richness in medium-sized fragments. Species richness of typical rainforest birds, in contrast, shows the more common trend of increase with area of fragments (Wiens 1989, Bolger *et al.* 1991, Newmark 1991, Bellamy *et al.* 1996, Turner 1996). This pattern is likely to

have been accentuated if sampling effort had been in proportion to area. Supplementary observations and earlier published records indicate that a number of carnivores, in particular, too rare to have been recorded in point count surveys are also largely confined to large fragments. This includes the Oriental Bay Owl and Spot-bellied Eagle Owl in Karian Shola (Kannan 1993, 1998, Mudappa 1998b), Mountain Hawk Eagle in Varagaliar (A. Kumar, personal communication), Blue-eared Kingfisher in Manamboli, and Rufous-bellied Eagle in Akkamalai (personal observations). Some of these species may require large forest areas due to their large home range requirements; for instance, Thiollay and Meyburg (1988) report that Rufous-bellied Eagles have home range sizes of 20 - 30 km² in Java and may not occur in forest patches smaller than 100 km².

On the other hand, only 11 bird species were seen occurring exclusively in fragments larger than 1,000 ha in this study. Of these, five were low-elevation birds (Jungle Owlet, Oriental Scops Owl, Dollarbird, Sri Lanka Frogmouth, White-bellied Woodpecker), and two were high-elevation species (Grey-breasted Laughingthrush, White-bellied Shortwing), that may occur in smaller fragments at the corresponding elevations (such fragments were not sampled during this study). The remaining five species were seen infrequently and their absence from even medium-sized fragments may indicate greater rarity rather than local extinction in such fragments.

The number of species in fragments was not a simple result of passive sampling of individual birds. This may be a realistic model in cases where a large habitat patch is suddenly broken up into islands (e.g., because of creation of a reservoir that floods low areas and leaves peaks as islands) and for species that are relatively sedentary or dispersal-limited. For habitat islands that were created long ago and vagile taxa like birds, however, even small islands will eventually be colonised or used for foraging and breeding. This may lead to higher number of individuals on the island than expected under area-based passive sampling. This scenario was modelled through the abundance-based passive sampling, a process similar to the *ecological drift* model proposed recently by Hubbell (2001), but the model failed to accurately predict the observed pattern of species richness.

The failure of the null models and the strong correlations between species richness and measures of habitat structure (particularly PC1) indicate that bird community structure in fragments is more strongly moulded by habitat change than by random-sampling dynamics and ecological drift. The observed species richness of the three largest fragments is 15 - 21% lower than expected under the abundance-based passive sampling model. This is mainly because many low-elevation species do not occur in the IYAK fragment and high-elevation species do not occur in KS and VA, although under the null model these inter-specific differences are ignored and all species are expected to occur in all fragments by chance alone. The disproportionately fewer species than expected in the smallest fragments (below a threshold area of 10 ha) is due to the additional process of local extinction of many rainforest bird species in these fragments because they contain insufficient area or habitat resources for those species. Similar results have been obtained for birds of urban chapparal fragments

in California (Bolger *et al.* 1991). The results suggest that models of fragmentation that do not consider all species or individuals as equivalent but allow species-specific variation in tolerance for fragment attributes are likely to be of greater predictive power.

6.5.3 Species turnover

Bird species turnover is likely to be mainly influenced by geographic factors under a system of non-equilibrium colonisation-extinction dynamics as proposed under the island biogeography theory of MacArthur and Wilson (1967) and the ecological drift model of Hubbell (2001). Fragments are likely to be more similar to each other in bird community composition the more similar they are in area and the closer they are to each other. On the other hand, community composition could be more deterministic, with species occurrences and abundances depending on site-specific habitat structure and resource availability. In a slash-and-burn habitat mosaic in tropical rainforests of northeast India, the degree of alteration of bird community composition in successional sites from primary forest was found to be strongly correlated to the degree of change in habitat structure and tree species composition of these sites as compared to primary forest (Raman *et al.* 1998).

In the Valparai landscape, both geographic and habitat factors influence bird species turnover. The similarity in bird community composition of rainforest fragments from the control site (IYAK) tended to decrease with increasing geographic distance from IYAK as well as with increasing difference in area with it. The effect of geographic distance is expected as fragments were often highly isolated by surrounding tea estates, plantations, or reservoirs, and the dynamics of fragments farther away is likely to have been independent of the control site. In addition, however, there was a significant influence of floristics—fragments that were similar in tree species composition with IYAK tended to also be similar in their bird communities. This is well illustrated by the Pannimade (PA) fragment, which was relatively undisturbed in habitat structure and tree species composition when compared to the control site. Although PA was the most isolated fragment (excluding the two northernmost fragments, VA and KS) from the control site, it was more similar to the control site than closer sites such as Puthuthottam. The influence of tree species composition on bird community composition is similar to the findings of Raman *et al.* (1998) along a rainforest successional gradient as well as the results reported in Chapter 4 and 5 from altitudinal and disturbance gradients in the Kalakad-Mundanthurai Tiger Reserve. This is possibly brought about by the occurrence of nectarivorous and frugivorous birds, which are likely to be directly related to the floristic composition, and even some insectivorous species, which may have specific tree species preferences for foraging (Robinson and Holmes 1984).

Determinism in species turnover is also revealed in the significant nested subset structure in bird community composition. Nested subset structure has been recorded in a wide variety of communities spanning taxonomic categories from butterflies to mammals and across temperate and

tropical regions (Wright *et al.* 1998). Such a pattern can emerge due to different processes: passive sampling, area or distance effects, and nestedness of microhabitats (Wright *et al.* 1998). Passive sampling is unlikely to be an explanation of the nestedness observed in this study. The passive sampling models that failed to predict observed patterns of species richness are unlikely to predict observed patterns of species composition. Under passive sampling, one would expect a positive relation between distribution and abunance, with abundant species represented in all fragments and rare species in fewer sites (Wright *et al.* 1998). In the present study, three ubiquitous species were among the most abundant ones (Plain Flowerpecker, White-cheeked Barbet, Greenish Leaf Warbler). However, other abundant species such as Yellow-browed Bulbul and Brown-cheeked Fulvetta did not actually occur in small fragments although they would be expected to occur under a passive sampling situation.

Area, at first, appears to be a major factor influencing nested subset structure. A number of species did not occur in fragments less than 10 ha in area. This area may have been insufficient to meet the home range requirements of species such as Malabar Trogon, Emerald Dove, Crested Serpent Eagle, and Greater Flameback. Other species absent from small fragments were those which probably had small home ranges; for example, six of the seven species of flycatchers recorded during the study from rainforests (the seventh species, Nilgiri Flycatcher, occurred but at lower densities, see Appendix 4). The absence of these birds and other small birds such as Dark-fronted Babbler, Large-billed Leaf Warbler, and Blackthraoted Munia, indicates that it is not area *per se* but probably the changes in habitat that lead to the selective local extinction of these species.

On the other hand, a majority of species occurred in medium-sized fragments (taken together and including those with relatively undisturbed rainforest vegetation such as Pannimade) as well as in large fragments. Many species that were apparently restricted to the largest fragments in this study may have been so restricted, not due to area limitation, but due to altitudinal distributions and habitat structure. These typically low- or high-elevation species may occur in fragments below 700 m or above 1,500 m, which could be confirmed for a few species during this study (Grey-breasted Laughingthrush, Whitebellied Shortwing).

Many species were probably responding more directly to habitat structure than area *per se*. For instance, the Malabar Trogon was seen only in the Pannimade fragment (10 ha) and the large fragments and not in any of the small or medium-sized fragments. This can be explained by the fact that only Pannimade and the large fragments had a relatively undisturbed rainforest habitat strcuture. That species may be nested in relation to other factors such as fragment isolation, habitat structure, or the nested distribution of microhabitats, with considerable variation across species and species categories, as noted in other studies also (Simberloff and Martin 1991, Kadmon 1995, Calmé and Desrochers 1999).

Nested subset structure and the high similarity in species composition among small fragments has implications for the SLOSS (single large or several small reserves) debate. The deterministic

pattern of species loss indicates that even a number of small, species-poor fragments, particularly those less than 10 ha, are likely to never contain all the species in a single large site (Bolger *et al.* 1991, Worthen 1996). It could be argued from the results of this study, however, that a set of medium-sized (10-100 ha) fragments could potentially harbour all the species found in an equivalent area of a single large fragment. This however may not be tenable in a landscape where there are only small or medium-sized fragments. Many of the species observed in small- or medium-sized fragments are individuals that are temporary visitors or settlers from adjoining large fragments. This is illustrated by the observation of Great Hornbills in a 7 ha fragment that was surrounded by shade-coffee and within flight distance (< 2 km) of other medium and large fragments. In the absence of large fragments in the landscape, further impoverishment of the bird communities of fragments is likely to occur, due to lack of source pools for species to disperse from.

6.5.4 Plantations and matrix tolerance

Tea and *Eucalytptus* plantations have a predominantly detrimental effect on rainforest birds being dominated by widespread, common, open-country bird species such as Red-whiskered Bulbul, Blyth's Reed Warbler, Ashy Prinia, and Common Tailorbird. Coffee plantations as they retain some shade trees support many more rainforest bird species. As none of the plantations support all rainforest bird species, the importance of retaining natural rainforest cover is paramount. Similar patterns have been noted by Daniels *et al.* (1990a) in bird communities in Uttara Kannada district. The influence of rainforest habitat structure and tree species composition on the rainforest bird community has been documented in earlier chapters (Chapters 4, 5). Among existing plantation areas, shade-coffee plantations resemble rainforest in structure and floristics to a greater extent than tea or *Eucalyptus*, thereby accounting for their greater bird diversity and similarity with primary rainforest. Measures to retain and encourage shade-coffee in preference to or in order to replace other sorts of plantations without native shade trees is therefore likely to have beneficial effects for bird conservation. Tea and shade-coffee plantations often abut protected areas all along the Western Ghats and these man-made habitats are used by many wildlife species. Given their location and areal coverage, these habitats, particularly shade-coffee plantations cannot be ignored for wildlife conservation policies.

The role of shade-coffee plantations in supporting many tropical forest birds has received much recent international attention (Greenberg *et al.* 1997a, b, Wunderle 1999, Sherry 2000). In the Anamalai hills, plantations, particularly shade-coffee, have beneficial effects on a number of rainforest bird species by allowing them to persist in small and medium-sized fragments, often at higher densities. This may be due to the ability of these species to exploit resources from the surrounding matrix to support higher populations within fragments. Another possibility is that following the local extinction of matrix-intolerant rainforest species, the remaining species increase in abundance due to density compensation effects. This process, along with the infiltration of open-

country species, may also explain the constancy of total bird density across the entire range of fragment sizes in this study.

6.5.5 Responses of bird species categories

Although responses of birds varied both within and across species categories, some broad patterns were evident. Among different diet-guilds, those that included many large and wide-ranging species appeared to be area-sensitive: bark-surface feeders, frugivores, and carnivores (woodpeckers, hornbills, imperial pigeons, hawks, and eagles). In addition, terrestrial insectivores too appeared to be area-sensitive, a pattern also noted in Amazonian tropical rainforest (Canaday 1996, Stratford and Stouffer 1999). The species richness of canopy and understorey insectivores, which constitute a sizable fraction of tropical rainforest bird communities, appeared to be related mainly to habitat structure. The availability of adequate foraging and nesting substrate may be more critical to these species than fragment area *per se*. Nectarivore species richness was unrelated to fragment area, possibly because these small-bodied species have small home range requirements, and even small fragments probably contained sufficient nectar and arthropod resources to meet their requirements. A similar pattern has been noted in Central Amazonia, where hummingbirds have been noted to be less susceptible to forest fragmentation (Stouffer and Bierregaard 1995b) than other guilds such as understorey or terrestrial insectivores (Stouffer and Bierregaard 1995a). Omnivores too, presumably because of their dietary flexibility, are widely distributed across fragment size classes, although more species occur at lower altitudes (as noted in Chapter 4) possibly due to higher productivity or availability of resources.

A result of particular conservation concern is the higher number of endemic and priority bird species in larger fragments. This underscores the need for maintenance of large tracts of tropical rainforest for bird conservation. As noted earlier, however, it is not merely area, but habitat structure that is also likely to be an important determinant of distribution and abundance of these species. It is likely that a greater number and abundance of endemic and priority species can be retained in the small and medium-sized fragments in the landscape, if the habitat was relatively undisturbed in these fragments.

6.5.6 Conservation implications

The conservation implications that emerge from the above results and discussion can be summarised in the following main points:

1. **ALASS, not SLOSS:** The guiding paradigm for conservation in fragmented landscapes should not be a debate over conservation of single large *or* several small reserves, but instead, emphasise the need to protect and conserve *all large and several small* remnants of natural habitat. This 'have the cake and eat it too' paradigm may seem unrealistic or impracticable in real-world

situations, but is certainly the target to aspire for. In the Anamalai hills, small (< 10 ha) and medium (10-100 ha) fragments play important roles in maintaining larger populations of rainforest birds in the landscape, providing habitat for altitudinal migrants, and increasing dispersal connectivity between areas. The conservation of fragments of all sizes cannot be ignored.

2. **Rainforest habitat restoration:** The deterioration of habitat structure in fragments due to disturbance has detrimental effects on rainforest birds. Many isolated fragments are now in a situation where mere protection will not suffice and is unlikely to result in full or rapid recovery. Active efforts to restore and improve rainforest habitat structure and tree species composition are needed for conservation of the rainforest bird community typical to the region. Many fragments currently continue to be disturbed due to removal of trees and fuelwood by local people. Conservationists, forest departments, and private companies and landowners need to work together to devise strategies and provide alternative fuel supplies for local people to reduce these impacts on fragments. Incentives for people to switch to liquefied petroleum gas available through outlets in Valparai need to be pursued urgently and vigorously.
3. **Role of shade-coffee plantations:** Coffee plantations with a mixture of native rainforest tree species in the canopy for shade are a relatively low-impact form of land-use, allowing the persistence of many rainforest birds within them as well as in adjacent fragments. Recent trends of conversion of shade-coffee to tea plantations in the Anamalai hills are, therefore, of great concern. Over the last two months as this chapter was written (August - September 2001), over 35 hectares of shade-coffee around the Korangumudi fragment have been completely cleared of all tree cover and planted with tea. There is an obvious need to curtail such transformations which have negative consequences in crucial conservation areas such as the Anamalai hills, not just locally but even at a landscape level. Also, there is a need to explore positive economic (tax, pricing) incentives for landowners to retain or enhance the area under such shade-coffee plantations in relation to areas under tea and *Eucalyptus*.
4. **Research needs:** Several questions remain before the effects of fragmentation on rainforest birds can be fully understood and effective management steps devised. This includes aspects known to have significant influences in other fragmented forests. Factors requiring study include edge effects, population trends and demography of birds in small and large fragments, effects of overstorey tree species composition in shade-coffee estates on bird community similarity with primary rainforest, bird community structure in fragments surrounded by different kinds of matrix habitats, influence of nest predation on species survival in fragments, and recovery of rainforest birds in restored areas.

6.6 SUMMARY

The conversion of large tracts of tropical rainforest to smaller patches embedded in a landscape matrix of human-altered habitats such as plantations is one of the serious and reigning concerns in the field of conservation biology. Here, the effects of rainforest fragmentation and conversion to tea, coffee, and *Eucalyptus* plantations on bird communities were studied in the highly man-modified landscape of the Anamalai hills in the southern Western Ghats. Systematic point-count sampling for birds and habitat sampling were carried out in the three plantations types and in 13 rainforest fragments ranging in area from 0.3 ha to 2,600 ha. A total of 106 bird species were recorded, including 75 typical rainforest species and 31 species of open-country and drier forests that had colonised disturbed fragments and plantations. Total bird species richness was higher in medium-sized fragments (10-100 ha), due to the entry of these widespread open-country species, along with the persistence of many rainforest species. Null models of passive sampling in relation to area or abundance did not predict bird species richness. Rainforest bird species richness instead increased virtually log-linearly with fragment area, with substantial decrease in species richness below a fragment area threshold of 10 ha. In addition, the structural development of rainforest canopy and vertical foliage distribution had positive effects on rainforest bird species. Medium-sized fragments, particularly with relatively undisturbed vegetation, held significant populations of rainforest bird species, including endemic species, and are important repositories and refuges in the landscape for birds. The similarity in bird community composition between sites was positively related to their similarity in tree species composition, and negatively with their difference in area or physical distance separating them. The compositional changes showed a nested-subset structure, indicating possible differential extinction of species in relation to changing area and habitat. Plantations, particularly of tea and *Eucalyptus*, detrimentally affected rainforest birds, although a number of rainforest birds thrived in shade-coffee plantations. Although 17 rainforest bird species did not occur in any plantations, those species that did occur also persisted or occurred at higher densities in small and medium-sized fragments in the landscape. The conversion of shade-coffee to tea plantations is a matter of concern for bird conservation in the region and needs to be offset through commercially viable incentives. The study also highlights the value of rainforest fragments and the need to reverse degradation through active efforts at restoring tree species composition and rainforest structure for rainforest bird conservation.

I am a part of all that I have met;
Yet all experience is an arch wherethro'
Gleams that untravelled world, whose margin fades
For ever and for ever when I move.

—*Ulysses* (Alfred, Lord Tennyson, 1809-1892)

CHAPTER 7

Concluding comments and synthesis

In this chapter, I briefly highlight key findings and conclusions regarding the community ecology and conservation of tropical rainforest bird communities in the Western Ghats, the details of which were presented in the earlier chapters. I then also attempt to point out some future research needs.

- The proper study and interpretation of bird community structure requires the use of appropriate methods to census birds. In the temperate region, the three most commonly used techniques of bird census are line transects, point counts, and territory spot-mapping. For tropical rainforests, particularly in south and south-east Asia, there have been few applications and assessments of different census techniques for use on bird communities. The effort made during this study to redress this lacuna (Chapter 3) suggests that, across species, the two methods most commonly used to census birds, namely line transects and point counts, yield density estimates of rainforest birds similar to, but slightly higher than, those obtained by more intensive spot-mapping. Estimates of relative abundance of bird species were similar in all three methods. Although spot-mapping is the method of choice for determining density and distributions of territorial birds, the point count technique was particularly suitable for application in this study. This was because it allowed a greater coverage of areas within the limited time, enabled obtaining replicate samples useful for statistical analyses, and helped survey birds in small fragments and rugged terrain with comparative ease. These advantages outweighed problems such as the possible overestimation of density of common bird species due to their mobility and inclusion cumulatively during the count period. There is a need to further test these methods for density comparisons between habitats and time periods. Point counts standardised for effort, in particular, may be useful for monitoring long-term trends of rainforest bird populations in rugged terrain and habitat remnants in the Western Ghats.

- The greater part of this study involved describing tropical rainforest bird community structure and its patterns of variation across a variety of settings. In Chapter 4, I attempted to describe how bird community structure varies along an elevational gradient in a landscape relatively undisturbed by human action (in the Kalakad-Mundanthurai Tiger Reserve). Although bird species richness was not found to vary substantially with elevation, there was pronounced turnover of bird species leading to community composition being very different at higher elevations as compared to lower elevations. The occurrence and turnover of species was correlated with elevation and tree species composition of these sites, did not appear to be due to stochastic factors. This argues for a significant influence of deterministic factors in bird community structure and weakens the possibility that rainforest bird communities are merely non-equilibrium communities produced by the chance assembly of species. The generality of this finding is supported by similar results obtained by some earlier studies as well as by the results in Chapter 5 and Chapter 6, which also argue for the importance of deterministic factors, particularly tree species composition and habitat structure, in determining rainforest bird community structure.

- Community ecologists have attempted to circumvent the difficulties of performing large-scale experimental studies or perturbations of community structure by developing procedures to simulate these processes using computers. It has often been suggested that patterns observed in nature may arise from the simple operation of chance factors (such as the random colonisation of a site by a set of species from a larger species pool) and such 'null' models may have to be first evaluated as the most parsimonious explanation for patterns. A hierarchy of null models, varying in complexity and in the number of constraints imposed, were evaluated to determine if observed patterns of community similarity between sites (Chapter 4) and species richness across fragments (Chapter 6) were reproduced under the operation of such chance or non-equilibrium dynamics. The results clearly suggest that null models with few or no constraints do not reproduce the observed patterns and trends. A degree of realism enters these models when biological constraints reflecting limitations of species richness at sites or the distributional ecology of species are factored in. The results therefore argue for a greater representation of biological constraints in future models and theoretical developments in the field of bird community ecology. These models need to build on the foundation of knowledge on the natural history and ecology of individual bird species.

- Earlier research has emphasised the value of lowland and low-elevation forests for conservation as these were believed to be areas containing the greatest number of species as well as species with narrowly-restricted ranges. The present study illustrates that in the Western Ghats, mid- and high-elevations (up to 1,400 m) may also have equivalent levels of bird diversity, and that endemic species with narrow ranges occur at both limits of the elevational gradient. The

substantial turnover in species with elevation suggests that areas encompassing all elevation zones must perforce be included for bird conservation to be effective. Of various habitat attributes, the maintenance of rainforest tree species composition at specific elevations appears particularly important for the maintenance of bird communities typical to the region.

- The alteration of rainforest habitat results in clear and discernible changes in bird community structure. At scales within that of a patch of secondary forest (Chapter 5) or fragment of rainforest (Chapter 6), bird species richness and community similarity with undisturbed rainforest are dependent strongly on habitat structural attributes such as woody plant density, canopy cover, and vertical stratification. This effect is at least partly mediated by the effects of habitat structure on bird abundance—with sites containing well developed habitat structure managing to support greater densities of rainforest birds. The bird species composition of such disturbed areas was again, as mentioned earlier, dependent on tree species composition besides other factors such as elevation and distance from the source pool. This has important implication as it indicates that even secondary forests and small fragments, particularly where they retain habitat structural and floristic attributes (e.g., Pannimade, 10 ha, Chapter 6), can act as refuges for rainforest birds in the landscape. Thus, direct efforts for bird conservation should include rainforest restoration efforts focussing on enhancing the structural and floristic resemblance of secondary forests and fragments with relatively undisturbed rainforest.

- At a larger spatial scale of the entire landscape too there are marked changes in the species pool and bird communities. In the rainforest-dominated landscape of the Agathyamalai hills, for instance, there were only two non-rainforest species that occurred only in disturbed or secondary rainforest habitats such as the abandoned plantations (Chapter 5). This is in sharp contrast to the highly man-modified landscape of the Anamalai hills, wherein there were at least 25 open-country species derived from drier deciduous forests and scrub jungles that had not only colonised plantations, but also used rainforest fragments (Chapter 6). Although the differences in species composition were partly due to the less disturbed habitat structure in the abandoned plantations in the Agasthyamalai region than in the rainforest fragments in the Anamalai hills, the effects of the larger landscape are also manifest.

- It is also clear from this study that all species are not equally susceptible to habitat alteration or fragmentation. The extent of change due to habitat alteration in bird species populations, assessed by the persistence index in this study, depended on attributes such as diet-guild, endemism, and body size. Various attributes of species influenced their persistence—species that are larger, rarer, or more restricted in distribution (endemics and priority species, Chapter 6) tended to be more vulnerable to human-induced habitat alteration. Species responses were also linked to their dietary ecology and habits—birds such as terrestrial insectivores, bark-surface feeders, carnivores, and

frugivores (Chapters 5 and 6) appeared to be more vulnerable to changes in the habitat. Such variations across species may be utilised to more effectively target conservation and monitoring efforts at the more vulnerable species.

- Landscapes such as the Anamalai ranges, containing fragments of rainforest in a matrix of plantations, pose several challenges for conservation. Where fragment size falls below a threshold of 10 ha, there are significant declines in rainforest bird species richness. Although medium-sized fragments (10 - 100 ha) may not contain all species, particularly large raptors, they hold populations of a majority of rainforest bird species. This is also true, to a lesser extent, of coffee estates that retain rainforest trees in the canopy for shade. As such sites help support larger populations of rainforest birds in man-modified landscapes, and increase connectivity between patches for wide-ranging birds and altitudinal migrants, they need to be included in bird conservation plans as potential refuges for birds.

- Several aspects pertinent to the study of rainforest bird communities remain to be elucidated., a few of which I consider particularly important are highlighted here. There is a need for further application and assessment of bird census methods and field techniques through comparisons between habitats and across years for particular species. Species vulnerable to habitat alteration, such as the Malabar Trogon, woodpeckers, terrestrial insectivores, and flycatchers, may be targeted for intensive ecological studies and monitoring. Territoriality, area-requirements, social organisation, multi-species flocking, behaviour, and plot occupancy patterns of virtually all resident rainforest bird species remains to be described and this will require in most cases the use of capture and ringing studies. There is also an urgent need to apply these techniques to monitor long-term trends in bird populations, to identify species that may be declining (towards extinction) and unravel underlying causes. The effects of elevation on bird communities need to be further explored by including areas at lower and higher elevations than was possible during this study. To what extent competition plays a role in community structure and elevational distribution patterns is also still an open question that could be the focus of fascinating studies. Studies on bird demography and dispersal are also needed to understand the processes underlying the colonisation and extinction of species, particularly in disturbed secondary habitats, regenerating or restoration areas, and rainforest fragments. This is also likely to yield insights into factors governing the temporal dynamics of bird communities. The effects of the surrounding landscape matrix on rainforest bird populations need to be explored across a variety of landscapes in the Western Ghats. At a much larger level, there is a need to compare bird communities of the Western Ghats with other tropical forest regions to see to what extent there are generalities, similarities, or divergences in bird community structure and its variation over space and time.

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APPENDIX 1

Bird species recorded within (+) and around (@) the Kalakad-Mundanthurai Tiger Reserve (KMTR) the Indira Gandhi Wildlife Sanctuary (IGWLS). Bird species occurring in undisturbed tropical rainforest are highlighted in grey. Some of these rainforest species also occur in other habitats, whereas others never occur in rainforests, except as vagrants or along edges and in disturbed patches.

S. No.	English Name	Scientific Name	KMTR	IGWLS	Source[a]
PHASIANIDAE (partridges, francolins, quails, and pheasants)					
1	Grey Francolin	*Francolinus pondicerianus*	+	+	
2	Rain Quail	*Coturnix coromandelica*	@		JJ/MK
3	Jungle Bush Quail	*Perdicula asiatica*	+	+	
4	Red Spurfowl	*Galloperdix spadicea*	+	+	
5	Painted Spurfowl	*Galloperdix lunulata*	+		
6	Grey Junglefowl	*Gallus sonneratii*	+	+	
7	Indian Peafowl	*Pavo cristatus*	+	+	
DENDROCYGNIDAE (whistling-ducks)					
8	Lesser Whistling-Duck	*Dendrocygna javanica*	@		JJ/MK
ANATIDAE (geese and ducks)					
9	Bar-headed Goose	*Anser indicus*	+		JJ/MK
10	Cotton Pygmy-Goose	*Nettapus coromandelianus*	@		JJ/MK
11	Spot-billed Duck	*Anas poecilorhyncha*	@		
12	Northern Pintail	*Anas acuta*	@		
13	Northern Shoveler	*Anas clypeata*		@	RK
TURNICIDAE (Buttonquails)					
14	Small Buttonquail	*Turnix sylvatica*	+		JJ/MK
15	Yellow-legged Buttonquail	*Turnix tanki*	+		
16	Barred Buttonquail	*Turnix suscitator*	+		JJ/MK
PICIDAE (wrynecks, piculets, and woodpeckers)					
17	Eurasian Wryneck	*Jynx torquilla*	+		JJ/MK
18	Speckled Piculet	*Picumnus innominatus*	+	+	
19	Rufous Woodpecker	*Celeus brachyurus*	+	+	
20	White-bellied Woodpecker	*Dryocopus javensis*	+	+	
21	Heart-spotted Woodpecker	*Hemicircus canente*		+	
22	Brown-capped Pygmy Woodpecker	*Dendrocopos nanus*	+	+	
23	Yellow-crowned Woodpecker	*Dendrocopos mahrattensis*		+	RK
24	Lesser Yellownape	*Picus chlorolophus*	+	+	
25	Streak-throated Woodpecker	*Picus xanthopygaeus*	+	+	
26	Common Flameback	*Dinopium javanense*	+	+	
27	Black-rumped Flameback	*Dinopium benghalense*	+	+	
28	Greater Flameback	*Chrysocolaptes lucidus*	+	+	
MEGALAIMIDAE (Asian barbets)					
29	Brown-headed Barbet	*Megalaima zeylanica*	+	+	
30	White-cheeked Barbet	*Megalaima viridis*	+	+	
31	Crimson-fronted Barbet	*Megalaima rubricapilla*	+	+	
32	Coppersmith Barbet	*Megalaima haemacephala*	+	+	
BUCEROTIDAE (hornbills)					
33	Malabar Grey Hornbill*	*Ocyceros griseus*	+	+	
34	Malabar Pied Hornbill	*Anthracoceros coronatus*	(?)	+	CRS
35	Great Hornbill	*Buceros bicornis*	+	+	
UPUPIDAE (hoopoes)					
36	Common Hoopoe	*Upupa epops*	+	+	
TROGONIDAE (trogons)					
37	Malabar Trogon	*Harpactes fasciatus*	+	+	

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CORACIIDAE (rollers)					
38	Indian Roller	*Coracias benghalensis*	+	+	
39	Dollarbird	*Eurystomus orientalis*		+	
ALCEDINIDAE (small kingfishers)					
40	Common Kingfisher	*Alcedo atthis*	+	+	
41	Blue-eared Kingfisher	*Alcedo meninting*		+	
42	Oriental Dwarf Kingfisher	*Ceyx erithacus*	+		
HALCYONIDAE (large kingfishers)					
43	Stork-billed Kingfisher	*Halcyon capensis*	+	+(CRS)	
44	White-throated Kingfisher	*Halcyon smyrnensis*	+	+	
45	Black-capped Kingfisher	*Halcyon pileata*	+		JJ/MK
CERYLIDAE (pied kingfishers)					
46	Pied Kingfisher	*Ceryle rudis*	+	+	
MEROPIDAE (bee-eaters)					
47	Blue-bearded Bee-eater	*Nyctyornis athertoni*		+	
48	Green Bee-eater	*Merops orientalis*	+	+	
49	Blue-tailed Bee-eater	*Merops philippinus*	+		
50	Chestnut-headed Bee-eater	*Merops leschenaulti*	+	+	
CUCULIDAE (old world cuckoos)					
51	Pied Cuckoo	*Clamator jacobinus*	+	+	
52	Chestnut-winged Cuckoo	*Clamator coromandus*	+	+	
53	Large Hawk Cuckoo[b]	*Hierococcyx sparverioides*	+	+	
54	Common Hawk Cuckoo	*Hierococcyx varius*	+	+	
55	Indian Cuckoo	*Cuculus micropterus*	+	+	
56	Lesser Cuckoo	*Cuculus poliocephalus*	+		
57	Banded Bay Cuckoo	*Cacomantis sonneratii*		+	
58	Grey-bellied Cuckoo	*Cacomantis passerinus*	+		
59	Drongo Cuckoo	*Surniculus lugubris*	+	+	
60	Asian Koel	*Eudynamys scolopacea*	+	+	
61	Blue-faced Malkoha	*Phaenicophaeus viridirostris*	+	+	
62	Sirkeer Malkoha	*Phaenicophaeus leschenaultii*	+	+	
CENTROPODIDAE (coucals)					
63	Greater Coucal	*Centropus sinensis*	+	+	
PSITTACIDAE (parrots)					
64	Vernal Hanging Parrot	*Loriculus vernalis*	+	+	
65	Rose-ringed Parakeet	*Psittacula krameri*	+		
66	Plum-headed Parakeet	*Psittacula cyanocephala*	+	+	
67	Malabar Parakeet*	*Psittacula columboides*	+	+	
APODIDAE (swifts)					
68	Indian Swiftlet	*Collocalia unicolor*	+	+	
69	White-rumped Needletail	*Zoonavena sylvatica*	+	+	
70	Brown-backed Needletail	*Hirundapus giganteus*		+	
71	Asian Palm Swift	*Cypsiurus balasiensis*	+	+	
72	House Swift	*Apus affinis*	+	+	
73	Fork-tailed Swift	*Apus pacificus*	+		
74	Alpine Swift	*Tachymarptis melba*	+	+	
HEMIPROCNIDAE (treeswifts)					
75	Crested Treeswift	*Hemiprocne coronata*	+	+	
STRIGIDAE (typical owls)					
76	Oriental Bay Owl	*Phodilus badius*	+	+	
77	Oriental Scops Owl	*Otus sunia*	+	+	
78	Collared Scops Owl	*Otus bakkamoena*	+	+	

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79	Eurasian Eagle Owl	*Bubo bubo*	+	+	
80	Spot-bellied Eagle Owl	*Bubo nipalensis*	+	+	
81	Brown Fish Owl	*Ketupa zeylonensis*	+	+	
82	Brown Wood Owl	*Strix leptogrammica*	+	(?)	
83	Jungle Owlet	*Glaucidium radiatum*	+	+	
84	Spotted Owlet	*Athene brama*	+	+	
85	Brown Hawk Owl	*Ninox scutulata*	+	+	
BATRACHOSTOMIDAE (Asian frogmouths)					
86	Sri Lanka Frogmouth	*Batrachostomus moniliger*	+	+	
EUROSTOPODIDAE (eared nightjars)					
87	Great Eared Nightjar	*Eurostopodus macrotis*		+	
CAPRIMULGIDAE (nightjars)					
88	Grey Nightjar	*Caprimulgus indicus*	+	+	
89	Large-tailed Nightjar	*Caprimulgus macrurus*	+	+	
90	Jerdon's Nightjar	*Caprimulgus atripennis*		+	
91	Indian Nightjar	*Caprimulgus asiaticus*	+		
COLUMBIDAE (pigeons and doves)					
92	Rock Pigeon	*Columba livia*	+	+	
93	Nilgiri Wood Pigeon*	*Columba elphinstonii*	+	+	
94	Mountain Imperial Pigeon	*Ducula badia*	+	+	
95	Laughing Dove	*Streptopelia senegalensis*	+	+	
96	Spotted Dove	*Streptopelia chinensis*	+	+	
97	Eurasian Collared Dove	*Streptopelia decaocto*	+	+	
98	Emerald Dove	*Chalcophaps indica*	+	+	
99	Pompadour Green Pigeon	*Treron pompadora*	+	+	
100	Yellow-footed Green Pigeon	*Treron phoenicoptera*	+		JJ/MK
RALLIDAE (rails, gallinules, and coots)					
101	Slaty-legged Crake	*Rallina euryzonoides*	+		
102	White-breasted Waterhen	*Amaurornis phoenicurus*	@	+	
103	Ruddy-breasted Crake	*Porzana fusca*		+	
104	Purple Swamphen	*Porphyrio porphyrio*	@		
105	Common Moorhen	*Gallinula chloropus*	@		
106	Common Coot	*Fulica atra*	@		
SCOLOPACIDAE					
(Subfamily Scolopacinae: snipes)					
107	Pintail Snipe	*Gallinago stenura*	+		JJ/MK
108	? Snipe	*Gallinago sp.*	+		
(Subfamily Tringinae: sandpipers)					
109	Green Sandpiper	*Tringa ochropus*	+		
110	Wood Sandpiper	*Tringa glareola*		+	RK
111	Common Sandpiper	*Actitis hypoleucos*	+	@	
BURHINIDAE (thick-knees)					
112	Eurasian Thick-knee	*Burhinus oedicnemus*	+		JJ/MK
CHARADRIIDAE					
(Subfamily Recurvirostrinae: stilts)					
113	Black-winged Stilt	*Himantopus himantopus*	+		
(Subfamily Charadriinae: plovers and lapwings)					
114	Little Ringed Plover	*Charadrius dubius*	+		JJ/MK
115	Yellow-wattled Lapwing	*Vanellus malabaricus*	+		JJ/MK
116	Red-wattled Lapwing	*Vanellus indicus*	+	+	
GLAREOLIDAE (coursers)					
117	Indian Courser	*Cursorius coromandelicus*	@		
LARIIDAE (terns)					

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118	River Tern	*Sterna aurantia*	+		JJ/MK
119	Common Tern	*Sterna hirundo*		@	RK
120	Whiskered Tern	*Chlidonias hybridus*	@		JJ/MK
ACCIPITRIDAE (ospreys, bazas, kites, hawks, eagles, harriers, buzzards, and vultures)					
121	Osprey	*Pandion haliaetus*	+	@	
122	Jerdon's Baza	*Aviceda jerdoni*	+	+	
123	Black Baza	*Aviceda leuphotes*	+	+	
124	Black-shouldered Kite	*Elanus caeruleus*	+	+	
125	Black Kite	*Milvus migrans*	+	@	
126	Brahminy Kite	*Haliastur indus*	+	+	
127	Grey-headed Fish Eagle	*Ichthyophaga ichthyaetus*	+	+	
128	Egyptian Vulture	*Neophron percnopterus*	@		JJ/MK
129	Red-headed Vulture	*Sarcogyps calvus*	@		JJ/MK
130	Short-toed Snake Eagle	*Circaetus gallicus*		+	RK
131	Crested Serpent Eagle	*Spilornis cheela*	+	+	
132	Black Eagle	*Ictinaetus malayensis*	+	+	
133	Pallid Harrier (?)	*Circus pygargus*	@(?)	(?)	
134	Crested Goshawk	*Accipiter trivirgatus*	+	+	
135	Shikra	*Accipiter badius*	+	+	
136	Besra	*Accipiter virgatus*	+	+	
137	Eurasian Sparrowhawk	*Accipiter nisus*	+		
138	Oriental Honey-Buzzard	*Pernis ptilorhynchus*	+	+	
139	White-eyed Buzzard	*Butastur teesa*		+	RK
140	Common Buzzard	*Buteo buteo japonicus*	+	+	
141	Long-legged Buzzard	*Buteo rufinus*	+		
142	Tawny Eagle	*Aquila rapax*	+		JJ/MK
143	Booted Eagle	*Hieraaetus pennatus*	+	+	
144	Rufous-bellied Eagle	*Hieraaetus kienerii*	+	+	
145	Changeable Hawk Eagle	*Spizaetus cirrhatus*	+	+	
146	Mountain Hawk Eagle	*Spizaetus nipalensis*		+	
FALCONIDAE (falcons)					
147	Kestrel	*Falco tinnunculus*	+	+	
148	Eurasian Hobby (?)	*Falco subbuteo*	(?)		
149	Laggar Falcon	*Falco jugger*	+		JJ/MK
150	Peregrine Falcon	*Falco peregrinus*		+	RK
PODICIPEDIDAE (grebes)					
151	Little Grebe	*Tachybaptus ruficollis*	@	@	
ANHINGIDAE (anhingas or darters)					
152	Darter	*Anhinga melanogaster*	+	@	
PHALACROCORACIDAE (cormorants)					
153	Little Cormorant	*Phalacrocorax niger*	+	@	
154	Great Cormorant	*Phalacrocorax carbo*	+	@	
ARDEIDAE (herons and bitterns)					
155	Little Egret	*Egretta garzetta*	@	@	
156	Great Egret	*Casmerodius albus*	@	@	
157	Intermediate Egret	*Mesophoyx intermedia*	@	@	
158	Cattle Egret	*Bubulcus ibis*	@	+	
159	Indian Pond Heron	*Ardeola grayii*	+	+	
160	Grey Heron	*Ardea cinerea*	+	@	
161	Little Heron	*Butorides striatus*	+	+(CRS)	
162	Black-crowned Night Heron	*Nycticorax nycticorax*	+		
163	Malayan Night Heron	*Gorsachius melanolophus*	+	+	
164	Black Bittern	*Dupetor flavicollis*	+	+(CRS)	

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THRESKIORNITHIDAE (ibises and spoonbills)					
165	Glossy Ibis	*Plegadis falcinellus*	@		JJ/MK
166	Black-headed Ibis	*Threskiornis melanocephalus*	@		
167	Black Ibis	*Pseudibis papillosa*	@		
168	Eurasian Spoonbill	*Platalea leucorodia*	@		JJ/MK
PELICANIDAE (pelicans)					
169	Spot-billed Pelican	*Pelecanus philippensis*	@		
CICONIDAE (storks)					
170	Painted Stork	*Mycteria leucocephala*	@		
171	Asian Openbill	*Anastomus oscitans*	@		
172	Woolly-necked Stork	*Ciconia episcopus*		@	RK
173	White Stork	*Ciconia ciconia*	+		JJ/MK
174	Lesser Adjutant	*Leptoptilos javanicus*		+	CRS
PITTIDAE (pittas)					
175	Indian Pitta[b]	*Pitta brachyura*	+	+	
IRENIDAE (fairy bluebirds and leafbirds)					
176	Asian Fairy Bluebird	*Irena puella*	+	+	
177	Blue-winged Leafbird	*Chloropsis cochinchinensis*	+		
178	Golden-fronted Leafbird	*Chloropsis aurifrons*	+	+	
LANIIDAE (shrikes)					
179	Brown Shrike	*Lanius cristatus*	+	+	
180	Bay-backed Shrike	*Lanius vittatus*	+		JJ/MK
181	Long-tailed Shrike	*Lanius schach*		+	
182	Southern Grey Shrike	*Lanius meridionalis*	+		JJ/MK
CORVIDAE					
(Subfamily Corvinae, tribe Corvini: treepies, crows)					
183	Rufous Treepie	*Dendrocitta vagabunda*	+	+	
184	White-bellied Treepie	*Dendrocitta leucogastra*	+	+	
185	House Crow	*Corvus splendens*	+	+	
186	Large-billed Crow	*Corvus macrorhynchos*	+	+	
(Subfamily Corvinae, tribe Artamini: woodswallows)					
187	Ashy Woodswallow	*Artamus fuscus*	+	+	
(Subfamily Corvinae, tribe Oriolini: orioles, cuckooshrikes, minivets, and flycacther-shrikes)					
188	Eurasian Golden Oriole	*Oriolus oriolus*	+	+	
189	Black-naped Oriole	*Oriolus chinensis*		+	RK
190	Black-hooded Oriole	*Oriolus xanthornus*	+	+	
191	Large Cuckooshrike	*Coracina macei*	+	+	
192	Black-headed Cuckooshrike	*Coracina melanoptera*	+	+	
193	Small Minivet	*Pericrocotus cinnamomeus*	+	+	
194	Scarlet Minivet	*Pericrocotus flammeus*	+	+	
195	Bar-winged Flycatcher-Shrike	*Hemipus picatus*	+	+	
(Subfamily Corvinae, tribe Dicrurini: drongos)					
196	Black Drongo	*Dicrurus macrocercus*	+	+	
197	Ashy Drongo[b]	*Dicrurus leucophaeus*	+	+	
198	White-bellied Drongo	*Dicrurus caerulescens*	+	+	
199	Bronzed Drongo	*Dicrurus aeneus*	+	+	
200	Spangled Drongo	*Dicrurus hottentottus*		+	
201	Greater Racket-tailed Drongo	*Dicrurus paradiseus*	+	+	
(Subfamily Corvinae, tribe Monarchini: monarchs)					
202	Black-naped Monarch	*Hypothymis azurea*	+	+	
203	Asian Paradise-Flycatcher	*Terpsiphone paradisi*	+	+	
(Subfamily Aegithininae: ioras)					

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204	Common Iora	*Aegithina tiphia*	+	+	
	(Subfamily Malaconotinae: woodshrikes)				
205	Large Woodshrike	*Tephrodornis gularis*	+	+	
206	Common Woodshrike	*Tephrodornis pondicerianus*	+	+	
MUSCICAPIDAE					
	(Subfamily Turdinae: thrushes and shortwings)				
207	Blue-capped Rock Thrush	*Monticola cinclorhynchus*		+	
208	Blue Rock Thrush	*Monticola solitarius*	+		JJ/MK
209	Malabar Whistling Thrush	*Myophonus horsfieldii*	+	+	
210	Pied Thrush[b]	*Zoothera wardii*	+		
211	Orange-headed Thrush	*Zoothera citrina*	+	+	
212	Scaly Thrush	*Zoothera dauma*	+	+	
213	Eurasian Blackbird	*Turdus merula*	+	+	
214	Whitebellied Shortwing*	*Brachypteryx major*	+	+	
	(Subfamily Turdinae, tribe Muscicapini: old world flycatchers)				
215	Asian Brown Flycatcher	*Muscicapa dauurica*	+	+	
216	Rusty-tailed Flycatcher[b]	*Muscicapa ruficauda*	+	+	
217	Brown-breasted Flycatcher[b]	*Muscicapa muttui*	+	+	
218	Red-throated Flycatcher	*Ficedula parva*	+		
219	Black-and-Orange Flycatcher*	*Ficedula nigrorufa*	+	+	
220	Verditer Flycatcher	*Eumyias thalassina*	+	+	
221	Nilgiri Flycatcher*	*Eumyias albicaudata*	+	+	
222	White-bellied Blue Flycatcher*	*Cyornis pallipes*	+	+	
223	Blue-throated Flycatcher	*Cyornis rubeculoides*	+	+	
224	Tickell's Blue Flycatcher	*Cyornis tickelliae*	+	+	
225	Grey-headed Canary Flycatcher	*Culicicapa ceylonensis*	+	+	
	(Subfamily Turdinae, tribe Saxicolini: chats)				
226	Indian Blue Robin[b]	*Luscinia brunnea*	+	+	
227	Oriental Magpie Robin	*Copsychus saularis*	+	+	
228	White-rumped Shama	*Copsychus malabaricus*		+	
229	Indian Robin	*Saxicoloides fulicata*	+	+	
230	Black Redstart	*Phoenicurus ochruros*	+		JJ/MK
231	Pied Bushchat	*Saxicola caprata*	+	+	
STURNIDAE (starlings and mynas)					
232	Chestnut-tailed Starling	*Sturnus malabaricus*	+	+	
233	Brahminy Starling	*Sturnus pagodarum*	+	+	JJ/MK, RK
234	Common Myna	*Acridotheres tristis*	+	+	
235	Jungle Myna	*Acridotheres fuscus*	+	+	
236	Hill Myna	*Gracula religiosa*	+	+	
SITTIDAE (nuthatches)					
237	Velvet-fronted Nuthatch	*Sitta frontalis*	+	+	
PARIDAE (penduline tits)					
238	Great Tit	*Parus major*		+	
239	Black-lored Tit	*Parus xanthogenys*	+	+	
HIRUNDINIDAE (swallows and martins)					
240	Eurasian Crag Martin (?)	*Hirundo rupestris*	(?)		JJ/MK
241	Dusky Crag Martin	*Hirundo concolor*	+	@	JJ/MK, RK
242	Barn Swallow	*Hirundo rustica*	+	+	
243	Pacific Swallow	*Hirundo tahitica*	+	+	
244	Wire-tailed Swallow	*Hirundo smithii*	+		JJ/MK
245	Red-rumped Swallow	*Hirundo daurica*	+	+	

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246	Northern House Martin	*Delichon urbica*	+		JJ/MK
PYCNONOTIDAE (bulbuls)					
247	Grey-headed Bulbul*	*Pycnonotus priocephalus*	+	+	
248	Black-crested Bulbul	*Pycnonotus melanicterus*	+	+	
249	Red-whiskered Bulbul	*Pycnonotus jocosus*	+	+	
250	Red-vented Bulbul	*Pycnonotus cafer*	+	+	
251	Yellow-throated Bulbul	*Pycnonotus xantholaemus*		+	RK
252	White-browed Bulbul	*Pycnonotus luteolus*	+	+	
253	Yellow-browed Bulbul	*Iole indica*	+	+	
254	Black Bulbul	*Hypsipetes leucocephalus*	+	+	
CISTICOLIDAE (cisticolas and prinias)					
255	Zitting Cisticola	*Cisticola juncidis*		@	RK
256	Grey-breasted Prinia	*Prinia hodgsonii*	+	+	
257	Jungle Prinia	*Prinia sylvatica*	+	+	
258	Ashy Prinia	*Prinia socialis*	+	+	
ZOSTEROPIDAE (white-eyes)					
259	Oriental White-Eye	*Zosterops palpebrosus*	+	+	
SYLVIIDAE					
(Subfamily Acrocephalinae: warblers)					
260	Grasshopper Warbler	*Locustella naevia*	+		
261	Blyth's Reed Warbler	*Acrocephalus dumetorum*	+	+	
262	Thick-billed Warbler	*Acrocephalus aedon*	+	+	
263	Booted Warbler	*Hippolais caligata*	+		JJ/MK
264	Common Tailorbird	*Orthotomus sutorius*	+	+	
265	Tickell's Leaf Warbler	*Phylloscopus affinis*		+	
266	Greenish Warbler[b]	*Phylloscopus trochiloides*	+	+	
267	Large-billed Leaf Warbler[b]	*Phylloscopus magnirostris*	+	+	
268	Western Crowned Warbler[b]	*Phylloscopus occipitalis*	+	+	
(Subfamily Megalurinae: grassbirds)					
269	Broad-tailed Grassbird*	*Schoenicola platyura*	+	+	
(Subfamily Garrulacinae: laughingthrushes)					
270	Wynaad Laughingthrush*	*Garrulax delesserti*	+	+	
271	Grey-breasted Laughingthrush*	*Garrulax jerdoni*	+	+	
(Subfamily Sylviinae, tribe Timaliini: babblers)					
272	Puff-throated Babbler	*Pellorneum ruficeps*	+	+	
273	Indian Scimitar Babbler	*Pomatorhinus horsfieldii*	+	+	
274	Tawny-bellied Babbler	*Dumetia hyperythra*	+	+	
275	Dark-fronted Babbler	*Rhopocichla atriceps*	+	+	
276	Yellow-eyed Babbler	*Chrysomma sinense*	+		
277	Rufous Babbler*	*Turdoides subrufus*	+	+	
278	Jungle Babbler	*Turdoides striatus*	+	+	
279	Yellow-billed Babbler	*Turdoides affinis*	+	+	
280	Brown-cheeked Fulvetta	*Alcippe poioicephala*	+	+	
(Subfamily Sylviinae, tribe Sylviini: *Sylvia* warblers)					
281	Orphean Warbler	*Sylvia hortensis*	+		JJ/MK
ALAUDIDAE (larks)					
282	Singing Bushlark	*Mirafra cantillans*	+		JJ/MK
283	Indian Bushlark	*Mirafra erythroptera*	+		JJ/MK
284	Rufous-winged Bushlark	*Mirafra assamica*		+	RK
285	Ashy-crowned Sparrow Lark	*Eremopterix grisea*	+	+	
286	Eurasian Skylark	*Alauda arvensis*	+		JJ/MK
287	Oriental Skylark	*Alauda gulgula*		+	RK

S. No.	English Name	Scientific Name	KMTR	IGWLS	Source[a]
NECTARINIIDAE					
(Subfamily Nectariniinae, tribe Dicaeini: flowerpeckers)					
288	Thick-billed Flowerpecker	*Dicaeum agile*	+	+	
289	Pale-billed Flowerpecker	*Dicaeum erythrorhynchos*	+	+	
290	Plain Flowerpecker	*Dicaeum concolor*	+	+	
(Subfamily Nectariniinae, tribe Nectariniini: sunbirds and spiderhunters)					
291	Purple-rumped Sunbird	*Nectarinia zeylonica*	+	+	
292	Crimson-backed Sunbird*	*Nectarinia minima*	+	+	
293	Purple Sunbird	*Nectarinia asiatica*	+	+	
294	Loten's Sunbird	*Nectarinia lotenia*	+	+	
295	Little Spiderhunter	*Arachnothera longirostra*	+	+	
PASSERIDAE					
(Subfamily Passerinae: sparrows)					
296	House Sparrow	*Passer domesticus*	+	+	
297	Chestnut-shouldered Petronia	*Petronia xanthocollis*	@		JJ/MK
(Subfamily Motacillinae: wagtails and pipits)					
298	Forest Wagtail[b]	*Dendronanthus indicus*	+	+	
299	White Wagtail	*Motacilla alba*	+		
300	White-browed Wagtail	*Motacilla maderaspatensis*	+	+	
301	Yellow Wagtail	*Motacilla flava*	+		JJ/MK
302	Grey Wagtail[b]	*Motacilla cinerea*	+	+	
303	Nilgiri Pipit*	*Anthus nilghiriensis*	+	+	
304	Paddyfield Pipit	*Anthus rufulus*	+	+	
(Subfamily Ploceinae: weavers)					
305	Baya Weaver	*Ploceus philippinus*	+		
(Subfamily Estrildinae: estrildine finches)					
306	Indian Silverbill	*Lonchura malabarica*	+	+	
307	White-rumped Munia	*Lonchura striata*	+	+	
308	Black-throated Munia	*Lonchura kelaarti*	+	+	
309	Scaly-breasted Munia	*Lonchura punctulata*	+		
310	Black-headed Munia	*Lonchura malacca*	+		JJ/MK
(Subfamily Fringillinae: finches)					
311	Common Rosefinch[b]	*Carpodacus erythrinus*	+	+	

* - endemic to the Western Ghats

[a] - Sources for species not recorded by the author: in KMTR (JJ: Joshua and Johnsingh 1998, MK: M. Katti *et al.* unpublished) and IGWLS (RK: Kannan 1998, CRS: Stonor 1946).

[b] - Winter migrants among rainforest birds.

APPENDIX 2

Range distribution and abundance (individuals/ha) of resident rainforest bird species in KMTR. Species are arranged increasing order of elevational mid-point. Rank refers to increasing correlation (Kendall Tau) between site elevation and abundance across sites A to N (see Chapter 4 for details of sites).

Common name	A	B	C	D	E	F	G	H	I	J	K	L	M	N	Tau	P	Rank
Large Woodshrike	0.1														-0.38	0.060	17
Grey-headed Bulbul*	0.1														-0.38	0.060	18
Loten's Sunbird	0.1														-0.38	0.060	19
Plum-headed Parakeet	0.1														-0.38	0.060	20
Rufous Babbler*	0.2														-0.38	0.060	21
Crimson-fronted Barbet	0.2	0.1		0.1											-0.58	0.004	10
Hill Myna	0.5	0.3	0.1	0.6											-0.62	0.002	6
Malabar Grey Hornbill*	0.6	0.2	0.2	0.4											-0.62	0.002	7
Bronzed Drongo	0.1			0.1											-0.43	0.033	15
Black-crested Bulbul	0.7	0.1		0.3	0.5										-0.56	0.006	12
Gold-fronted Leafbird	0.3	0.1	0.1		0.1										-0.64	0.001	4
White-bellied Treepie	0.6	0.6	0.5	1.8	0.8	0.7									-0.59	0.004	9
Asian Fairy Bluebird	1.0	1.1	0.5	0.9	0.6	0.8	0.8								-0.69	0.001	3
Malabar Parakeet*	0.8	0.5	0.3	0.8	0.2	0.2	0.6								-0.71	0.000	1
Black-naped Monarch	0.3	0.3	0.4	0.4	0.9		0.1								-0.58	0.004	11
Rufous Woodpecker	0.1				0.1	0.2	0.1	0.1	0.1	0.1					-0.21	0.291	28
Besra	0.2	0.1	0.1				0.1				0.1				-0.45	0.026	14
Greater Racket-tailed Drongo	2.0	1.1	1.1	1.2	1.1	0.4	0.5	0.4	0.2	0.7	0.5				-0.70	0.000	2
Vernal Hanging Parrot	0.8	0.4		0.1		0.4	0.3		0.1		0.1	0.1			-0.43	0.034	16
White-bellied Blue Flycatcher*	1.1	0.7	0.7	1.1	0.8	1.1	0.3		0.1		0.4	0.2	0.1		-0.53	0.009	13
Greater Flameback	0.7	0.5	0.7	0.3	0.1		0.2	0.5	0.3	0.1	0.4	0.4	0.3	0.3	-0.23	0.254	27
Mountain Imperial Pigeon	0.8	1.5	1.5	1.3	0.3	0.1	0.2							0.2	-0.63	0.002	5
Grey Junglefowl	0.5	0.2	0.7	0.6	0.4	0.1	0.1	0.2	0.3	0.1				0.1	-0.62	0.002	8
Crimson-backed Sunbird*	3.1	2.8	3.2	3.3	3.0	2.7	2.9	3.2	1.2	2.8	2.9	3.1	0.4	1.2	-0.37	0.065	22
Malabar Trogon	0.3	0.5	0.3		0.2	0.2		0.3	0.2	0.1	0.2		0.1	0.2	-0.35	0.080	23
Puff-throated Babbler	0.4	0.5	0.8	0.9	0.3	0.5	0.3	0.4	0.9	0.2	0.5	0.2	0.4	0.3	-0.28	0.162	24
White-cheeked Barbet	0.5	1.0	0.3	0.7	0.1	0.4	1.2				0.1	0.1	0.3	0.3	-0.27	0.171	25
Yellow-browed Bulbul	1.3	2.1	2.3	1.8	2.3	2.4	2.8	1.0	0.6	0.6	1.1	1.6	1.1	1.1	-0.26	0.203	26

Common name	A	B	C	D	E	F	G	H	I	J	K	L	M	N	Tau	P	Rank
Scarlet Minivet	0.9	0.4	0.7	0.1	0.4	0.8	1.0	0.2	0.4		0.2	0.3	0.5	0.7	-0.12	0.543	29
Velvet-fronted Nuthatch	0.5	0.8	0.2	0.3	0.5			0.3	0.3	0.1	0.3	0.2	0.4	0.8	-0.02	0.910	33
Brown-cheeked Fulvetta	1.0	3.3	1.7	2.0	2.0	2.3	2.7	4.3	3.5	4.0	1.8	1.9	3.0	1.4	0.12	0.547	36
Malabar Whistling Thrush	0.4	0.3	0.4	0.4	0.1	0.2	0.2	0.8	0.3	0.5	0.4	1.1	0.4	0.4	0.24	0.240	39
Crested Serpent Eagle												0.1			0.26	0.192	40
Plain Flowerpecker	0.1	0.3	0.5	0.4	0.3	0.3	1.0	0.6	0.4	0.3	0.1	0.6	0.7	0.9	0.33	0.104	42
Little Spiderhunter	0.1	0.2	0.2	0.2			0.3	0.9	0.4	0.7	0.2	0.5	0.4	0.5	0.46	0.023	49
Indian Scimitar Babbler	0.3	0.1	0.3	0.4	0.9	0.6	0.6	1.2	1.1	0.9	0.8	0.4	1.1	1.1	0.49	0.014	50
Wynaad Laughingthrush*		1.4			5.0			0.8	0.8					1.0	-0.03	0.887	32
Common Flameback			0.1	0.1		0.1		0.1	0.2	0.1	0.1				-0.01	0.944	34
White-bellied Woodpecker				0.1						0.1					-0.04	0.831	30
Red Spurfowl (a)							0.1								-0.03	0.885	31
Dark-fronted Babbler		0.1	0.5				0.2		0.5	0.8	0.4	0.2	0.4	0.4	0.35	0.080	43
Emerald Dove			0.1			0.1		0.2	0.2	0.1		0.1	0.1	0.1	0.36	0.072	45
Black-throated Munia			0.2											0.2	0.09	0.670	35
Orange-headed Thrush			0.1	0.1		0.1		0.2	0.2	0.4	0.4	0.1	0.1	0.2	0.55	0.006	53
Black Bulbul					0.2	0.1	0.6	0.7	1.8	1.7	0.2	0.7	1.3	1.1	0.66	0.001	56
Oriental White-eye					0.8	1.2	3.1	6.1	5.7	5.0	6.2	11	8.9	7.6	0.83	0.000	58
Bar-winged Flycatcher-shrike						0.2	0.2	0.5	0.2	0.5	0.2	0.2	0.4	0.8	0.70	0.000	57
Eurasian Blackbird (b)										0.1					0.15	0.469	37
Grey-headed Canary Flycatcher							0.4	3.0	1.8	2.6	2.2	1.8	1.8	2.8	0.64	0.001	55
Oriental Dwarf Kingfisher											0.1				0.20	0.311	38
Black-lored Tit (c)								0.1	0.2	0.4	0.1	0.3	0.1		0.51	0.012	51
Nilgiri Flycatcher*								1.2	0.8	0.4		0.1	0.6	1.1	0.52	0.010	52
Black-and-Orange Flycatcher*								1.8	1.2	1.9	0.8	0.2	1.4	2.5	0.63	0.002	54
Grey-breasted Laughingthrush*									0.4					2.2	0.36	0.076	44
Speckled Piculet											0.1			0.1	0.43	0.033	48
Red-whiskered Bulbul (d)													0.3		0.32	0.111	41
Malayan Night Heron														0.1	0.38	0.060	46
White-bellied Shortwing*														0.3	0.38	0.060	47

* Species endemic to Western Ghats; + species not detected in point counts but occurrence confirmed from opportunistic surveys (or, in rare species, assumed to have been missed). **Incomplete data:** (a) also occurs sporadically in elevations below site G, more infrequently above, (b) also occurs in higher elevation sites, (c) vagrant, seen only once during the study, (d) a non-forest species, occurring at the rainforest edge only in the slightly disturbed site M.

APPENDIX 3

Bird species and abundances (indivduals/ha) in the plantations, edges, logged and rainforest sites in and around KMTR.

Species	Body mass (g)	5-year abandoned plantations			15-year abandoned plantations	Edges			Logged	Primary rainforests					
		P1	P2	P3	P7	P4	P5	P6	T7	T3	T4	T5	T8	T9	T10
Red Spurfowl	369			0.10						0.10					
Grey Junglefowl	750				0.10	0.10	0.20			0.10			0.31	0.20	0.10
Speckled Piculet	11.5				0.10						0.20				
Rufous Woodpecker	101									0.10			0.10	0.10	0.10
White-bellied Woodpecker	300														0.10
Common Flameback	101	0.10		0.10		0.20					0.10		0.20	0.10	0.10
Greater Flameback	150	0.20	0.31	0.10	0.31	0.31	0.31	0.10	0.20	0.20	0.41	0.41	0.31	0.51	0.10
White-cheeked Barbet	80.5	0.66	0.31	0.41	0.15	0.20	0.05	0.05	0.20	1.02	0.05	0.10			
Malabar Trogon	82		0.10	0.20		0.10	0.10		0.10		0.20		0.20	0.31	0.10
Oriental Dwarf Kingfisher	15										0.05				
Vernal Hanging Parrot	20	0.10	0.10	0.05		0.15				0.25	0.05	0.05	0.05		
Malabar Parakeet*	85			0.15						0.61					
Mountain Imperial Pigeon	620					0.10				0.20					
Emerald Dove	132					0.05			0.05			0.05	0.15	0.10	0.10
Crested Serpent Eagle	1300											0.05			
Besra	135		0.05			0.10		0.10		0.05	0.10				
Asian Fairy Bluebird	120				0.20	0.10	0.20			0.81					
White-bellied Treepie	99.25						0.41								
Scarlet Minivet	25	0.10		0.10		0.92	0.71	0.10	0.36	0.97	0.20	0.31	0.36	0.20	
Bar-winged Flycatcher-Shrike	9		0.31	0.31	0.92			0.61	0.31	0.15	0.15	0.15	0.15	0.46	0.46
Greater Racket-tailed Drongo	79.5		0.25	0.20	0.10	0.56	0.56	0.20		0.51	0.56		0.20	0.41	0.71
Black-naped Monarch	11				0.05					0.05					
Malabar Whistling Thrush	116.9	0.41	0.46	0.71	0.20	1.07	0.56		0.25	0.20	0.41	1.07	0.31	0.76	0.51
Pied Thrush	58.6			0.10											
Orange-headed Thrush	53.3	0.05	0.10		0.10			0.05	0.05		0.41	0.05	0.20	0.20	0.36

Species	Body mass (g)	5-year abandoned plantations			15-year abandoned plantations	Edges			Logged	Primary rainforests					
		P1	P2	P3	P7	P4	P5	P6	T7	T3	T4	T5	T8	T9	T10
Eurasian Blackbird	75														0.05
Rusty-tailed Flycatcher	13.3	0.15	0.05	0.05	0.05					0.10					
Black-and-Orange Flycatcher*	8.5				0.31			0.51	1.02		0.81	0.20	1.22	1.83	1.83
Nilgiri Flycatcher*	17.5				1.22			0.31	0.41			0.10	0.81	1.22	0.41
White-bellied Blue Flycatcher*	19.9	0.10	0.05	0.31		0.20	0.31		0.10	0.31	0.25	0.20	0.10		
Grey-headed Canary Flycatcher	6.5	1.32	1.53	0.81	0.31	0.71	0.71	0.92	1.32	0.41	2.24	1.83	1.83	2.95	2.65
Indian Blue Robin	18			0.10						0.20				0.05	0.05
Hill Myna	126						0.15								
Velvet-fronted Nuthatch	11.7	0.25	0.36		0.71	0.10	0.25	0.25	0.31		0.25	0.15	0.31	0.25	0.10
Black-lored Tit	14.4	0.20	0.51	0.10	0.41	0.31		0.41	0.10		0.10	0.31	0.20	0.10	0.41
Red-whiskered Bulbul	27.4							0.92	0.20						
Yellow-browed Bulbul	31	0.87	0.46	0.92	1.73	1.78	2.24	0.87	0.76	2.75	1.07	1.73	0.56	0.97	0.56
Black Bulbul	42.9	1.07	1.22	1.38	4.74	2.14	1.53	2.60	1.07	0.61	0.15	0.76	1.83	0.76	1.68
Oriental White-Eye	8.75	3.97	8.45	6.16	6.62	5.14	11.41	6.11	6.42	3.06	6.21	11.3	5.65	6.06	4.99
Blyth's Reed Warbler	10.6							0.15	0.05						
Greenish Warbler	7	0.46	0.51	0.36	1.22	0.05		0.51	0.31	0.41	0.05		0.36	0.10	0.15
Large-billed Leaf Warbler	11.5	0.31	0.20	0.20	0.36			0.31	0.36	1.02	0.05		0.56	0.61	0.31
Wynaad Laughingthrush*	90						0.81						0.76	0.76	
Grey-breasted Laughingthrush*	55												0.41		
Puff-throated Babbler	26	0.20	0.10	0.05		0.25	0.25	0.05	0.31	0.31	0.41	0.15	0.81	0.36	0.10
Indian Scimitar Babbler	47.8	0.31	0.71	0.36	0.92	1.07	0.15	0.71	0.76	0.56	0.76	0.41	1.07	1.17	0.87
Dark-fronted Babbler	16		0.15		0.92	0.15		0.46	0.31	0.15	0.31	0.15	0.46		0.61
Brown-cheeked Fulvetta	20.7	0.76	0.36	0.56	0.97	1.88	1.88	1.43	2.14	2.70	1.78	1.94	3.46	4.33	4.02
Plain Flowerpecker	6.2	0.15	0.20	0.25	0.51	0.20	0.81	0.76	0.51	1.02	0.10	0.56	0.41	0.56	0.25
Crimson-backed Sunbird*	4.5	1.38	1.99	1.68	0.61	2.04	1.53	2.44	0.31	2.90	2.85	3.06	1.17	3.00	2.80
Little Spiderhunter	13	0.36	0.56	0.31	0.87	0.66	0.15	0.71	0.25	0.25	0.20	0.46	0.41	0.92	0.71
Grey Wagtail	16.3							0.05							0.05

* Species endemic to the Western Ghats.

APPENDIX 4

Densities of birds (individuals/ha) across the 13 rainforest fragments in the Anamalai hills (names in Chapter 6). Western Ghats endemics are marked (*). Habitat preferences: RF = rainforest birds, OC = Open-country birds. *N* = Number of detections (encounters) of species across sites in point-count surveys.

Species	K2	K1	V4	V3	PA	TF	KO	PU	AN	MA	KS	VA	IYAK	Habitat	*N*
Ashy Drongo	0.32	0.18	-	-	0.25	0.04	0.38	0.04	-	-	0.03	-	-	RF	15
Asian Fairy Bluebird	-	-	0.42	0.13	0.25	0.42	-	0.13	0.12	0.99	0.57	0.93	0.34	RF	65
Asian Paradise Flycatcher	-	-	-	-	0.13	0.04	0.13	0.04	-	-	0.03	0.08	0.02	RF	12
Bar-winged Flycatcher-Shrike	0.32	-	-	0.06	0.3	0.08	0.3	0.13	0.18	-	0.06	0.04	0.17	RF	23
Besra	-	-	-	-	0.13	-	-	-	-	-	0.03	-	0.07	RF	8
Black Bulbul	-	-	-	0.06	0.04	-	-	-	1.88	0.03	-	-	1.53	RF	81
Black Eagle	-	-	-	-	0.04	-	-	-	0.06	-	-	-	-	RF	2
Black-and-Orange Flycatcher*	-	-	-	-	-	0.08	-	-	0.52	-	-	-	0.54	RF	32
Black-crested Bulbul	-	-	-	0.51	-	0.42	-	-	0.06	0.28	0.25	0.34	-	RF	23
Black-lored Tit	-	0.36	-	0.13	0.25	0.3	0.38	0.13	0.36	0.06	-	0.08	0.14	RF	24
Black-naped Monarch	-	-	-	-	0.64	0.17	0.21	-	0.12	0.28	-	0.85	0.25	RF	54
Black-throated Munia	-	-	-	-	-	-	-	-	-	-	-	-	0.19	RF	3
Bronzed Drongo	-	0.73	-	0.51	0.47	0.59	0.68	1.06	0.06	0.71	0.22	0.3	-	RF	60
Brown Fish Owl	-	-	-	0.06	-	-	-	-	-	-	-	-	-	RF	1
Brown-breasted Flycatcher	-	-	-	-	0.04	-	0.04	-	-	-	-	-	0.02	RF	3
Brown-cheeked Fulvetta	-	-	-	0.45	3.73	0.55	0.93	0.51	3.76	2.63	0.25	3.61	2.94	RF	86
Chestnut-winged Cuckoo	-	-	-	-	-	-	-	-	-	-	-	-	0.02	RF	1
Common Flameback	-	-	-	-	0.17	-	0.13	0.34	-	0.31	0.13	0.17	0.03	RF	20
Crested Serpent Eagle	-	-	-	-	-	-	0.08	-	-	-	0.03	0.04	0.02	RF	5
Crimson-backed Sunbird*	0.32	0.36	-	0.64	2.25	1.78	0.34	0.89	1.18	1.7	0.19	1.36	1.66	RF	266
Crimson-fronted Barbet	-	-	-	0.38	-	0.08	0.04	0.81	0.24	0.28	0.64	0.59	-	RF	41
Dark-fronted Babbler	-	0.55	1.06	0.76	0.21	1.4	-	-	0.33	0.37	0.06	0.13	0.15	RF	30
Dollarbird	-	-	-	-	-	-	-	-	-	-	-	0.13	-	RF	3
Emerald Dove	-	-	-	-	-	0.13	0.08	0.04	-	0.28	-	-	0.03	RF	15
Eurasian Blackbird	0.64	-	-	-	-	0.13	-	-	0.03	-	-	-	0.12	RF	9

Species	K2	K1	V4	V3	PA	TF	KO	PU	AN	MA	KS	VA	IYAK	Habitat	*N*
Forest Wagtail	-	-	0.21	-	-	-	-	-	-	0.17	0.03	0.04	-	RF	9
Golden-fronted Leafbird	-	-	-	0.13	-	0.13	0.17	0.08	-	-	-	-	-	RF	6
Great Hornbill	-	-	-	0.13	-	-	-	0.04	0.09	0.08	0.16	-	0.14	RF	11
Greater Flameback	0.64	-	-	0.25	0.34	0.25	0.47	0.17	0.24	0.42	0.19	0.51	0.27	RF	46
Greater Racket-tailed Drongo	-	-	-	0.32	1.23	0.3	0.13	0.08	-	0.76	1.4	1.57	0.15	RF	87
Greenish Leaf Warbler	0.32	1.09	1.27	0.83	1.4	0.85	1.4	1.53	1.06	0.45	0.32	0.42	0.73	RF	262
Grey Junglefowl	-	-	-	0.19	0.25	-	-	0.13	0.21	0.23	0.48	0.04	0.22	RF	34
Grey Wagtail	-	-	-	-	-	-	0.04	-	0.03	0.03	-	-	0.02	RF	4
Grey-breasted Laughingthrush*	-	-	-	-	-	-	-	-	-	-	-	-	0.17	RF	1
Grey-headed Canary Flycatcher	-	-	-	-	-	-	0.08	0.13	1.58	0.06	-	-	1.41	RF	74
Heart-spotted Woodpecker	-	-	-	-	-	-	0.08	-	-	0.06	0.25	0.17	-	RF	8
Hill Myna	-	-	-	0.13	0.85	0.3	0.25	1.32	-	0.59	0.45	1.36	0.44	RF	82
Indian Blue Robin	0.32	0.55	-	0.25	0.21	0.13	0.17	0.08	0.09	0.28	0.03	-	0.12	RF	43
Indian Scimitar Babbler	1.27	0.73	-	1.02	1.57	0.55	0.34	1.15	0.79	0.62	0.06	0.51	0.75	RF	98
Jerdon's Baza	-	-	-	-	-	-	-	-	-	0.03	-	-	-	RF	1
Jungle Owlet	-	-	-	-	-	-	-	-	-	0.06	-	0.08	-	RF	2
Large Hawk Cuckoo	-	-	-	-	-	-	0.04	-	-	0.03	-	-	-	RF	2
Large Woodshrike	0.32	-	-	-	0.13	0.38	0.76	0.3	-	0.11	0.06	0.17	0.07	RF	35
Large-billed Leaf Warbler	-	-	-	0.25	0.76	0.38	-	0.38	0.55	0.34	0.54	0.25	0.49	RF	121
Lesser Yellownape	-	0.18	-	-	-	-	-	0.04	-	-	0.06	-	-	RF	3
Little Spiderhunter	-	-	-	0.06	0.42	0.76	0.21	0.34	0.15	0.74	-	0.55	0.27	RF	83
Malabar Grey Hornbill*	-	0.18	0.21	0.19	0.17	0.08	0.34	0.25	-	0.59	1.4	0.76	0.07	RF	78
Malabar Parakeet*	0.32	1.64	1.91	0.06	-	0.81	-	-	-	0.85	0.6	0.55	-	RF	47
Malabar Trogon	-	-	-	-	0.17	-	-	-	-	0.17	0.22	0.25	0.07	RF	15
Malabar Whistling Thrush	-	0.55	0.21	0.25	0.85	0.47	0.25	0.81	0.33	1.16	0.92	1.1	0.42	RF	147
Mountain Imperial Pigeon	0.32	-	0.85	0.06	-	0.21	-	0.08	0.18	0.14	0.45	0.17	0.61	RF	58
Nilgiri Flycatcher*	-	-	-	0.06	0.47	-	0.17	0.08	0.76	-	-	-	0.73	RF	69

Species	K2	K1	V4	V3	PA	TF	KO	PU	AN	MA	KS	VA	IYAK	Habitat	*N*
Orange-headed Thrush	0.64	0.55	-	0.32	0.42	0.08	0.13	0.47	0.49	0.34	0.57	0.21	0.2	RF	83
Oriental Scops Owl	-	-	-	-	-	-	-	-	-	-	0.03	-	-	RF	1
Oriental White-Eye	3.82	2.36	3.18	0.13	2.33	2.38	3.14	1.15	5.46	1.05	-	-	3.89	RF	117
Plain Flowerpecker	0.95	1.09	1.27	1.27	1.61	1.66	1.15	1.32	0.91	1.3	0.32	1.32	0.87	RF	270
Pompadour Pigeon	-	-	-	-	-	-	-	0.34	-	0.08	0.38	0.17	-	RF	11
Puff-throated Babbler	0.64	-	0.42	0.64	0.13	0.81	0.17	0.68	0.45	0.79	0.54	0.3	0.34	RF	116
Red Spurfowl	-	0.36	-	0.25	0.25	0.13	0.08	-	0.09	0.06	0.03	-	0.03	RF	15
Rufous Babbler	1.59	0.73	-	-	-	-	0.81	0.76	-	-	0.13	-	-	RF	13
Rufous Woodpecker	-	-	-	-	-	-	0.34	-	-	-	-	0.08	-	RF	5
Rusty-tailed Flycather	-	-	-	-	0.25	0.13	-	0.17	-	0.25	-	0.08	-	RF	24
Scaly Thrush	-	-	-	-	-	-	-	-	-	-	-	0.04	-	RF	1
Scarlet Minivet	-	-	2.33	0.83	0.17	0.25	0.98	1.06	0.52	0.54	0.45	0.64	0.37	RF	53
Sri Lanka Frogmouth	-	-	-	-	-	-	-	-	-	-	0.03	-	-	RF	1
Velvet-fronted Nuthatch	1.27	0.73	-	0.19	0.81	0.47	1.27	1.44	0.88	0.14	0.06	0.42	0.63	RF	76
Vernal Hanging Parrot	0.64	0.55	-	0.19	0.25	0.3	0.89	0.13	-	0.42	0.19	0.34	0.08	RF	68
Western Crowned Warbler	-	-	-	-	0.25	-	0.34	0.21	0.3	-	-	-	0.1	RF	5
White-bellied Blue Flycatcher	-	-	-	-	0.25	0.17	-	0.08	0.09	0.65	1.08	0.38	0.1	RF	50
White-bellied Shortwing*	-	-	-	-	-	-	-	-	-	-	-	-	0.19	RF	11
White-bellied Treepie	-	-	-	-	-	-	-	0.08	-	0.2	0.6	0.25	-	RF	16
White-bellied Woodpecker	-	-	-	-	-	-	-	-	-	-	0.06	0.08	-	RF	2
White-cheeked Barbet	0.95	1.46	1.06	0.7	0.51	0.51	0.55	1.49	0.61	1.24	0.45	0.51	0.51	RF	165
Wynaad Laughingthrush*	-	-	-	-	-	0.34	-	-	-	-	0.25	0.34	0.41	RF	5
Yellow-browed Bulbul	-	-	0.85	0.76	1.61	1.36	0.34	0.85	2.09	1.33	1.72	1.36	1.49	RF	215
Ashy Prinia	-	-	-	-	-	-	0.13	-	-	-	-	-	-	OC	1
Asian Brown Flycatcher	-	-	-	0.06	-	-	0.08	0.04	-	-	-	-	-	OC	4
Black-rumped Flameback	-	-	0.42	-	0.17	-	0.25	-	-	-	0.03	-	-	OC	7
Black-shouldered Kite	-	-	-	-	-	-	0.08	-	-	-	-	-	-	OC	2

Species	K2	K1	V4	V3	PA	TF	KO	PU	AN	MA	KS	VA	IYAK	Habitat	*N*
Blyth's Reed Warbler	1.27	0.91	1.49	0.83	0.21	0.59	1.91	0.38	0.03	-	0.06	-	0.08	OC	110
Booted Eagle	-	-	-	-	-	-	0.04	-	-	-	-	-	-	OC	1
Brown Shrike	-	-	-	-	0.04	-	0.34	0.08	-	-	-	-	-	OC	11
Brown-capped Pygmy Woodpecker	-	-	-	0.13	-	-	-	-	-	-	-	-	-	OC	1
Chestnut-headed Bee-Eater	-	-	-	-	-	-	-	-	-	0.23	-	0.21	-	OC	7
Chestnut-tailed Starling	0.95	-	-	-	-	-	-	-	-	-	-	-	-	OC	1
Common Hoopoe	-	-	-	-	-	-	0.13	-	-	-	-	-	-	OC	3
Common Iora	-	-	-	0.38	0.17	0.42	0.17	0.08	-	-	0.03	-	-	OC	14
Common Rosefinch	0.32	0.18	-	0.13	-	-	0.08	-	-	-	-	-	-	OC	4
Common Tailorbird	1.27	0.91	1.27	0.51	-	0.08	0.68	0.42	-	-	-	-	-	OC	33
Eurasian Golden Oriole	-	-	0.21	-	-	-	-	-	-	0.08	-	0.04	-	OC	5
Great Tit	-	-	-	-	-	-	-	-	-	-	0.06	-	-	OC	1
Greater Coucal	0.32	-	0.21	0.13	0.04	-	0.17	0.17	0.03	-	0.06	0.04	-	OC	17
Grey-breasted Prinia	-	-	-	-	-	-	0.25	-	-	-	-	-	-	OC	3
House Crow	-	0.18	-	0.19	-	-	-	-	-	-	-	-	-	OC	3
Jungle Myna	1.27	-	-	-	-	-	-	-	-	-	-	-	-	OC	3
Large-billed Crow	0.32	0.18	0.21	0.64	0.76	1.74	0.42	1.78	0.06	0.11	0.45	0.04	0.12	OC	62
Oriental Magpie Robin	-	0.36	-	-	-	-	0.13	0.13	-	-	-	-	-	OC	5
Plum-headed Parakeet	2.23	0.36	-	-	-	0.08	0.64	0.51	-	0.34	0.22	0.08	-	OC	29
Purple Sunbird	0.64	-	0.85	0.57	-	-	0.04	-	-	-	-	-	-	OC	10
Red-whiskered Bulbul	3.82	1.09	2.97	2.55	0.08	0.68	2.93	0.64	0.06	-	0.19	-	0.14	OC	93
Shikra	-	-	-	-	-	-	0.08	-	-	-	-	-	-	OC	1
Small Minivet	1.59	-	-	0.25	0.08	-	0.21	-	-	-	-	-	-	OC	6
Spotted Dove	-	0.36	-	-	-	-	-	-	-	-	-	-	-	OC	1
Streak-throated Woodpecker	0.64	-	-	-	-	-	-	0.08	-	-	-	-	-	OC	2
White-breasted Waterhen	-	-	-	0.06	-	-	-	-	-	-	-	-	-	OC	1
White-throated Kingfisher	-	-	-	-	-	-	0.08	-	-	-	-	-	-	OC	2

Plate 1

Rainforest landscape of the Kalakad-Mundanthurai Tiger Reserve as seen from Sengaltheri.

Landscape of rainforest fragments with tea estates in Andiparai, Anamalai ranges.

Plate 2

A view of the canopy in relatively undisturbed rainforest in Sengaltheri, Kalakad-Mundanthurai Tiger Reserve.

A five-year abandoned cardamom plantation in Sengaltheri, KMTR.

Plate 3

A small rainforest fragment (K2) in the Anamalai hills with adjoining road, tea estate, and *Eucalyptus* plantation.

Akkamalai—the largest rainforest fragment in the Anamalai hills with grasslands at the higher elevations.

Addendum: Author's Note

The PDF file of this thesis was prepared in June 2022 using Word document files from 2001. All efforts have been made to ensure that the contents and page numbers match the original thesis, but it is possible that a couple of minor differences exist compared to the original document:

> Raman, T. R. S. 2001. Community ecology and conservation of tropical rainforest birds in the southern Western Ghats, India. PhD thesis, Indian Institute of Science, Bangalore. Pages iv +182 + 3 plates.

— T. R. Shankar Raman, 3 July 2022, Valparai.